University of Alberta

Spatial scale and temporal variability of songbird population dynamics in the boreal mixedwood forests of northern Alberta.

by

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Abstract

I studied the population dynamics of songbirds at two sites in the boreal mixedwood forest of northern Alberta. I first confirmed that point counts are an unbiased index of density. I then proposed appropriate spatial scales for the study of population dynamics and estimated these for 28 species. I estimated the minimum scale of synchrony in population dynamics using a clustering technique and a randomization test, and estimated the maximum scale using a spline correlogram. Population dynamics in 14 of 25 species examined were synchronous over areas $\geq 100 km^2$. I attempted to determine what mechanisms might have induced synchrony in population dynamics over these scales by correlating changes in density with factors postulated to work *via* two mechanisms. I found that both Moran effects and dispersal may be important in synchronizing population dynamics over these scales. The implications of this work for researchers designing monitoring programs or experiments is also discussed.

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Chapter 1: Introduction

Population ecology is the study of how and why the density of populations vary in time and space. This thesis is concerned with several aspects of the population ecology of songbirds in the boreal mixedwood forests of northern Alberta. In particular, I was interested in how the population dynamics of songbirds varied in space. Instead of focusing on a few focal species, I examined dynamics in all species that were sufficiently common to adequately model. As a result, this thesis includes analyses of 28 species found at two sites in the boreal mixedwood forests of northern Alberta: Calling Lake and Meanook. Thus, I hope my results are general enough to provide some insight into the population dynamics of this songbird community as a whole.

Since an accurate population census of the songbirds was not available, I wanted to examine changes in density in space and time using point counts. Point counts provide only an index of density. In order to measure changes in population density in space and time, I first needed to ensure that the relative efficiency of this technique did not depend on true population density. Thus, in Chapter 2, I assessed whether point counts were a biased index of true abundance. I also determined whether the maximum or mean number of individuals observed at a point count station during each breeding season was a better index of changes in true abundance.

Having decided how to measure changes in population densities, Chapter 3 then established a theoretical basis for choosing an appropriate spatial scale to study population dynamics. I also empirically estimated such scales for 25 species at the Calling Lake site (Chapter 3) and for 13 species at Meanook (Appendix 3).

Chapter 3 established that the population dynamics of 15 species were synchronous over large spatial scales ($\geq 100 km^2$). In Chapter 4, I attempted to determine what mechanisms might have induced synchrony in population dynamics over these scales.

Finally, this work has implications for researchers designing monitoring programs or experiments. In Chapter 5, I address how this work is relevant for the design of effective and efficient sampling designs for songbirds, and provide some recommendations.

Chapter 2: Does detectability of boreal songbirds depend on density?

Introduction

When studying patterns of abundance, it is important to verify that no systematic errors are influencing the observed patterns. Thompson (2002) divides variation in estimates of abundance into spatiotemporal variation (often the component of interest to the researcher), bias (systematic under or over counting) and random variation. Although point counts are the most common technique for surveying birds, they provide at best an index of the number of birds in the area surveyed (Rosenstock *et al.* 2002). If counts are to be compared, the resulting bias (undercounting) must be consistent in time and space; i.e. the number of individuals observed must be linearly related to the true abundance (Link and Nichols 1994, Johnson 1995, Pollock *et al.* 2002, Rosenstock *et al.* 2002, Thompson 2002).

Several studies have suggested that this assumption may be violated for songbirds. Typically, the vast majority of individuals observed during a point count survey are detected aurally (Gibbs and Wenny 1993, Rosenstock *et al.* 2002); therefore, changes in song output and environmental variables influencing observer efficiency can significantly affect detectability (Mackowicz 1974, Bart and Shoultz 1984, Verner 1985, Gibbs and Wenny 1993, Schieck 1997, Rosenstock *et al.* 2002). High population densities may increase territorial behaviours such as singing (Mönkkönen and Aspi 1997), potentially introducing bias into any index of abundance based on aural detections.

We also know that the bias of a sample depends on the dispersion pattern within the sampling unit, being unbiased only when individuals are evenly distributed (Mönkkönen and Aspi 1997). Given that dispersion patterns change with density, since less favorable habitats are more likely to be occupied only at high densities (Mönkkönen and Aspi 1997, Chamberlain and Fuller 1999), bias of point-count surveys may depend on population density.

In this study, I wanted to test whether point counts are unbiased estimators of true abundance. Thus, I quantified the potential bias in measurements of bird abundance, so I could clearly separate spatio-temporal variation from other sources of variation. Double sampling can be used to quantify the accuracy and precision of index counts. All points are surveyed using an index technique (e.g. point counts), while a subset of these points is surveyed with an intensive technique that provides an accurate count of all individuals present (Bart and Earnst 2002). True abundance can then be predicted from the index counts by fitting an appropriate model (Eberhardt and Simmons 1987, Thompson 1992, Johnson 1995, Bart and Earnst 2002). I compared estimates of abundance from an intensive survey method, spot mapping (a territory mapping method), with estimates of abundance from point count surveys. Although spot mapping does not always identify all individuals present (Gibbs and Wenny 1993), it is generally considered a better approximation of a true census of birds (Verner 1985).

I wanted to find a suitable double-sampling model for correcting point-count estimates of birds in the boreal mixedwood. In particular, I determined if a linear model was appropriate, so that index counts could be compared in time or space without correction. I also wanted to determine if territory size influenced the accuracy of point-count estimates. Since the probability of detecting an individual is reduced if only a fraction of its territory is sampled, and the area surveyed around point-count stations was less than the territory size of some songbirds, I predicted that species with smaller territories would have a stronger correlation in abundance estimates derived from the two survey techniques. Finally, I also compared models with mean and maximum point-count abundance observed during a breeding season to determine which was more closely related to spot-mapping abundance.

Methods

Study Area

This study uses a subset of data from the Calling Lake Fragmentation Study (Schmiegelow *et al.* 1997; Schmiegelow & Hannon 1999), located in north-central

Alberta, Canada (55° N, 113° W; Figure 2.1). The study area encompasses approximately 14,000 ha of boreal mixedwood forest, dominated by old (80-130) aspen (*Populus tremuloides*) stands. Some white spruce (*Picea glauca*) and black spruce (*Picea mariana*) are also present. For this paper, I used 108 stations that were surveyed using point counts and spot mapping from 1993 through 1996 (Figure 2.1).

Sampling Design

This survey was not designed to compare estimates from the two survey techniques, introducing some limitations and complications into the analyses. Point-count stations were 100m radius plots located on a 200m grid (Schmiegelow *et. al.* 1997). Each station was surveyed for five minutes five times each breeding season (every ten days from the third week of May through late June). The first survey period was ignored in this study because most migrants were not yet breeding. More details of the sampling design are available in Schmiegelow *et. al.* (1997).

Point count and spot mapping surveys (F. Schmiegelow and M.-A. Villard, unpublished data) were conducted separately, so the observations of the number of individuals were considered to be independent. Spot mapping observer or experimental treatment effects (i.e. control, fragment, riparian) appear to be negligible when plotted (Toms, unpublished results), and were ignored in this study. Twenty-one spot-mapping grids of three sizes were used: 10 ha (3 grids), 20 ha (15 grids) and 25ha (3 grids). Each spot-mapping grid contained some fraction of 2-12 point count stations. Spot mapping started at dawn and finished within 5 hours. The observer walked through the grid slowly (at a pace of approximately 15-17 minutes per 400m of transect, if possible). Eight rounds of spot mapping were conducted during the breeding season (between the last week of May and the first week of July). All rounds were used to provide a single estimate of territory locations. Territories were delineated following Bibby *et al.* (1992) and International Bird Census Committee (1969). Only birds with delineated territories were included in analyses. Different subsets of the grids were surveyed each year, although some grids were surveyed for several years (up to four years).

Data

I focused on twelve species that were relatively abundant in the surveyed plots: Black-capped Chickadee (*Poecile atricapillus)*, Black-throated Green Warbler (*Dendroica virens)*, Connecticut Warbler (*Oporornis agilis)*, Least Flycatcher (*Empidonax minimus)*, Mourning Warbler (*Oporornis philadelphia)*, Ovenbird (*Seiurus aurocapillus)*, Red-breasted Nuthatch (*Sitta canadensis)*, Red-eyed Vireo (*Vireo olivaceus)*, Rose-breasted Grosbeak (*Pheucticus ludovicianus)*, Western Tanager (*Piranga ludoviciana)*, White-throated Sparrow (*Zonotrichia albicollis)* and Yellow-rumped Warbler (*Dendroica coronata)*. Independent estimates of territory sizes were obtained from the Birds of North America series (Morse 1993, Pitochelli 1993, Smith 1993, Briskie 1994, Falls and Kopachena 1994, Van Horn and Donovan 1994, Pitochelli *et al.* 1997, Hunt and Flaspohler 1998, Ghalambor and Martin 1999, Hudon 1999, Cimprich *et al.* 2000, Wyatt and Francis 2002). If a range of territory sizes was given, the midpoint of the range was used for the statistical analyses.

Two indexes of abundance for each species were derived from point-count data: mean numbers of individuals counted at each station in rounds two through five, and maximum numbers of individuals counted at each station in any of rounds two through five. True abundance was estimated as the number of individuals with at least half their spot-mapped territory intersecting an individual point count plot.

Statistical Analyses

Double sampling aims to estimate true abundance from indices of abundance (Bart and Earnst 2002). I fit linear double-sampling models, and then examined the residuals to confirm these models were appropriate. Since the indices are counts, in this case, I would have liked to linearize them with a log transformation. However, this is a non-linear transformation of an estimated parameter and could result in biased estimates. Using a jackknife estimator will reduce this bias (Mooney and Duval 1993):

$$\tilde{X}_i = \frac{1}{n}\sum_{m \in s} \ln(\hat{X}_i^{(-m)} + 0.1), \qquad (1)$$

where s is the sample, $\hat{X}_i^{(-m)}$ is the mean or maximum abundance calculated over all rounds excepting round m. I added 0.1 to deal with zero values.

The jackknifed variance estimate of $\tilde{X}_i$ (under sampling with replacement) is:

$$v(\tilde{X}_i) = \frac{1}{n(n-1)} \sum_{m \in s} [\ln(\hat{X}_i^{(-m)} + 0.1) - \tilde{X}_i]^2 \qquad (3)$$

Although the jackknife estimators were very strongly correlated with the simple non-jackknifed log transformations in the surveyed data (Appendix 1), this might not be true for all data. Furthermore, it provides an estimate of sampling variation that is otherwise difficult to obtain for the maximum point count index.

One further complication results from the nature of the sampling design: the study was not designed to compare estimates from spot-mapping and point-count surveys, so spot-mapping grids did not neatly coincide with point-count stations. Instead, point-count stations intersected the spot-mapping grid to different extents, depending on the sample plot. Therefore, point-count observations were weighted by the proportion of the station within the plot, ω_i, and $\omega_i \tilde{X}_i$ was used as the explanatory covariate in all analyses.

Several double-sampling models were evaluated. The simplest model assumed that the relationship between point-count abundance and number of territories did not depend on the spatial location of the spot-mapping grid or on the year. Note that the response variable (the number of territories) is also a count so generalized linear models were required. The other models included random effects of space or time: point-count stations were grouped in space or time and all stations within the group were assumed to have the same double-sampling relationship. Essentially, this technique models abundances at individual point-count stations as deviations from the spot-mapping grid or year averages. The second model grouped stations in space by including a random intercept associated with the spot-mapping grid. The third model grouped stations in time by including a random intercept associated with year.

All models were fit to the data as generalized linear mixed models using the NLMIXED procedure of SAS version 8.2. Unfortunately, there is no technique to find maximum likelihood estimates for these models when we allow $\tilde{X}_i$ to be an estimate with associated error. Therefore, we must assume that it is measured without error even though we know this is not the case. This probably results in a slight underestimate of

the slope parameter (Davies and Hutton 1975). Furthermore, SAS only allows models with random effects on a single level, so models incorporating both space and time as main effects could not be fit. Akaike weights (derived from AIC values) were used to determine the relative merits of each model. These weights are a measure of the weight of evidence that a given model is the best in the set evaluated (Anderson *et al.* 2000). Plots of residuals were examined for evidence of non-linearity.

Finally, I tested the prediction that species with smaller territories would have a stronger correlation in estimates from the two survey techniques by examining whether model fit was influenced by territory size. Vonesh and Chinchilli (1997) suggest the use of r_c, a model concordance coefficient, as a measure of model fit. r_c ranges from –1 to 1: a perfect model fit corresponds to $r_c = 1$, and a significant lack of fit corresponds to $r_c \leq 0$. Thus larger values of r_c correspond to better model fits and my prediction would be supported if territory size was negatively correlated with r_c. Spearman rank correlations were used to test this prediction.

Results

The number of territories from spot mapping was plotted against jackknife estimates of point-count abundance (Figure 2.2 and Appendix 1). Most species show at best a weak relationship between the number of territories and the jackknife estimators at the scale of a point-count station; Least Flycatcher was the only species with a moderately strong linear relationship. For most species, this relationship was stronger when I compared equivalent statistics calculated at the spot-mapping grid scale (i.e. summing across stations within a grid; Figure 2.3 and Appendix 1). This suggests that sampling variation of some sort is obscuring the underlying relationship.

These results suggested that estimators incorporating the effects of space or time might be an improvement, if some of the sampling error was due to pseudoreplication or other spatial or temporal effects. In fact, Akaike weights clearly indicated that models incorporating spatial location were better for most species than fixed models or models

incorporating time (Tables 2.1 and 2.2). Residual plots show no evidence of non-linearity (Toms, unpublished results), so linear models are appropriate.

Maximum and mean point-count abundance generally had similar results. However, the maximum point-count generally produced better model fits as measured by r_c (Table 2.1) and had slopes that were closer to one (Table 2.2). As predicted, there was a significant negative correlation between territory size and model fit (as measured by r_c; ρ =-0.61, p=0.04 for maximum point-count; ρ =-0.62, p=0.04 for mean-point count).

Discussion

This paper attempted to determine whether point counts are a reasonable index of true abundance in boreal mixedwood forests. At the scale of a spot-mapping grid (typically 10-20ha in forest; Bibby *et al.* 1992), many studies have compared point-count or line-transect surveys and spot mapping (e.g. Emlen 1971, Franzreb 1976, Frochot *et al.* 1977, Svensson 1981, Szaro and Jakle 1982, Cyr *et al.* 1995). As with others (Svensson 1981, Cyr *et al.* 1995), I found total abundance across several point-count stations to be positively correlated with the number of territories. However, consistency at this spatial scale did not hold at smaller spatial scales.

At the scale of a single point-count station (3.1 ha), both maximum and mean point counts were linearly related to the number of territorial individuals. Slopes that are quite different from one can be problematic, because changes in the index are not indicative of the true changes in abundance. In fact, the double-sampling models for most species did not have slope parameters significantly different from zero, indicating that there was no significant relationship between point-count abundance and spot-mapping abundance at the point-count station scale. Maximum point-counts were a more sensitive index of abundance, with slopes closer to one. Maximum point-counts also tended to fit a little better than mean point-counts, although all models had only poor to moderate fits. Thus, maximum point-counts appear to be a somewhat better index than mean point-counts for the species examined here. The differences in slopes observed between species may reflect behavioural differences; for example, both sexes of Least Flycatcher are known to

sing and singing rates are thought to be very high (averaging 49 songs/minute; Briskie 1994) and their estimated slope was very high (Table 2.2).

Interestingly, when I fit similar models defining the number of territorial individuals as the number of territories overlapping the point-count station to any extent, fits were much improved as measured by r_c (Appendix 2). Songbirds often sing more at the edges of their territories than in the centers (e.g. Hudon 1999, Cimprich *et al.* 2000), and point counts may be a better index of territory edges than of the number of individuals with territories located in the plot. Because most registrations in point counts are of singing males (Gibbs and Wenny 1993, Rosenstock *et al.* 2002), this suggests that point counts may be more representative of territorial boundaries than of the territories themselves. Thus, species with less of their boundary in the point count station (i.e. species with large territories) would not be as effectively surveyed using point counts. In fact, I did find that model fits were negatively correlated with territory size.

My results suggest that point counts are associated with significant sampling errors at the scale of a 100m radius plot, except for Least Flycatcher. Correlations between point counts and spot mapping are known to be stronger in species with substantial spatial or temporal variations in abundance (Svensson 1981, DeSante 1986), possibly because sampling variance then forms a smaller proportion of the total variance. In this study, Least Flycatcher territories were found only in limited parts of the spot-mapping grids (i.e. they were spatially clustered, as also found by Sherry and Holmes 1985), which may have contributed to their stronger relationship at the point-count station scale. They also have the smallest territory of the species studied, and species with smaller territories had a stronger relationship between point-count and spot-mapping abundance.

Results from four other studies that have been conducted at the scale of an individual point-count station are mixed (DeSante 1981, 1986, Tarvin *et al.* 1998, Jones *et al.* 2000). Fixed-radius and variable-radius point counts were linearly correlated with the density of breeding pairs of Blue Jay (*Cyanocitta cristata*; Tarvin *et al.* 1998) and Cerulean Warblers (*Dendroica cerulea*; Jones *et al.* 2000), and significant linear correlations were found between variable-radius point-count abundance and spot mapping for five of eight species in California scrubland (DeSante 1981). However, even with an inflated sample

size due to pseudoreplication, only seven of nineteen species surveyed in Californian subalpine forests showed significant positive correlations (DeSante 1986). Furthermore, six of these species had very clumped distributions across the site, increasing the apparent correlation because of the high number of absences. The evidence to date thus suggests that individual point-count stations are not consistently effective in estimating the density of territorial individuals.

Individual point-count stations may not reflect density of territorial individuals because they also detect non-territorial individuals ("floaters") and individuals moving outside their territorial boundaries (Granholm 1983, Verner 1985). Here, models which included effects of spatial location were a significant improvement over models that ignored such effects, i.e. fits were improved when abundances at individual point-count stations were modelled as deviations from grid averages. Extra-territorial movement of individuals within a spot-mapping grid could explain this result. However, the relative efficiency of each survey technique could vary for many other reasons: differences in observer efficiency (although the point count survey rotated observers to reduce this possibility; Bibby *et al.* 1992), presence of background noise at some locations (e.g. due to a creek or gas pipeline compressor), differences in vegetation (e.g. shrubby plots may be more difficult to survey than open areas; Mackowicz 1977, Schieck 1997), or even differences in bird communities (e.g. some species with loud songs could reduce the likelihood of hearing a quiet species). Models with random effects of year were not supported by the data, so detectability did not significantly differ across the four years of the study.

In this study, spot mapping was presumed to be an unbiased, precise measure of true abundance. However, spot mapping also relies on aural detections for delineating territory boundaries, and can be subject to sampling or observer error (Verner 1985, Verner and Milne 1990). Even if the number of territories is correctly determined by spot mapping, their locations are often slightly offset from territories obtained by following colour-banded individuals (Enemar *et al.* 1979, Tiainen and Bastian 1983). If estimated territory locations were shifted from their true locations, it would affect the degree of overlap between spot-mapped territories and point-count abundance and influence the results of this study.

In conclusion, there is no evidence to suggest that point-count abundance is not linearly related to the number of territorial individuals, for the twelve species examined. In other words, there is no evidence that detectability of point counts depends on density of the population. If such a relationship had been found, future analyses would have required correction of each estimate using an appropriate double-sampling model. Since this was not the case, indices of abundance from point counts can be compared across time or space without correction, as long as relative measures of abundance are sufficient.

Maximum point-counts appear to be a better index than mean point-counts for the species examined. However, both indices appear to have large sampling errors. I found that spatial location could account for some of this variability. Therefore, correcting for spatial location may be worthwhile, if the reduction in variance is large enough to offset the difficulties of fitting and using a more complicated model. Single point-count stations were poorly correlated with abundance from spot mapping, except for Least Flycatcher. Therefore, the use of isolated point-count stations in monitoring schemes is not recommended, unless they have previously been shown to be a valid index for a given species. Finally, model fits were better for species with smaller territories, suggesting we should avoid using point counts to monitor species with large territories.

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Table 2.1. Akaike weights and r_c values for the three generalized linear models fitting spot-mapping abundance as a function of point-count abundance at the Calling Lake study area: a model with only fixed effects, a model including a random effect of spot-mapping grid, and a model including a random effect of year. Akaike weights represent the probability that a given model is the best in the set tested; r_c values are a measure of model fit, where a perfect fit corresponds to $r_c = 1$, and a significant lack of fit corresponds to $r_c \leq 0$. The best-fitting model in the set is in bold type.

		No Random		Grid Random		Year Random	
Species	Point Count Index	Akaike weight	r_c	Akaike weight	r_c	Akaike weight	r_c
Black-capped Chickadee	Maximum	**0.54**	**0.01**	0.26	0.05	0.20	0.01
	Mean	**0.54**	**0.01**	0.26	0.04	0.20	0.01
Black-throated Green Warbler	Maximum	0.03	0.19	**0.94**	**0.32**	0.03	0.22
	Mean	0.00	0.12	**1.00**	**0.30**	0.00	0.14
Connecticut Warbler	Maximum	0.00	0.07	**1.00**	**0.27**	0.00	0.09
	Mean	0.00	0.03	**1.00**	**0.27**	0.00	0.05
Least Flycatcher	Maximum	**0.53**	**0.80**	0.28	0.80	0.19	0.80
	Mean	0.13	0.66	**0.82**	**0.73**	0.05	0.66
Mourning Warbler	Maximum	0.33	0.01	**0.55**	**0.07**	0.12	0.01
	Mean	0.30	0.00	**0.60**	**0.07**	0.11	0.00
Ovenbird	Maximum	**0.58**	**0.09**	0.21	0.09	0.21	0.09
	Mean	**0.58**	**0.07**	0.21	0.09	0.21	0.07
Rose-breasted Grosbeak	Maximum	0.02	0.01	**0.93**	**0.24**	0.04	0.08
	Mean	0.02	0.00	**0.93**	**0.23**	0.05	0.07
Red-breasted Nuthatch	Maximum	0.15	0.02	**0.76**	**0.16**	0.08	0.06
	Mean	0.16	0.01	**0.72**	**0.15**	0.12	0.06
Red-eyed Vireo	Maximum	0.00	0.02	**1.00**	**0.20**	0.00	0.02
	Mean	0.00	0.02	**1.00**	**0.21**	0.00	0.02
Western Tanager	Maximum	0.22	0.00	**0.60**	**0.14**	0.17	0.05
	Mean	0.22	0.00	**0.60**	**0.14**	0.17	0.05
White-throated Sparrow	Maximum	0.00	0.01	**1.00**	**0.23**	0.00	0.01
	Mean	0.00	0.01	**1.00**	**0.22**	0.00	0.01
Yellow-rumped Warbler	Maximum	0.12	0.01	**0.58**	**0.13**	0.30	0.09
	Mean	0.13	0.01	**0.56**	**0.12**	0.31	0.08

Table 2.2. Parameter estimates for best-fitting model of spot-mapping abundance as a function of point-count abundance at the Calling Lake study area. The set of models tested were: a model with only fixed effects, a model including a random effect of spot-mapping grid, and a model including a random effect of year.

Species	Point Count Index	Best Model	α		β		random effect	
			estimate	SE	estimate	SE	estimate	SE
Black-capped Chickadee	Max.	fixed only	-1.57	0.27	0.26	0.22	-	-
	Mean	fixed only	-1.56	0.30	0.24	0.23	-	-
Black-throated Green Warbler	Max.	grid	-0.55	0.17	0.58	0.13	0.44	0.16
	Mean	grid	-0.51	0.20	0.48	0.13	0.55	0.18
Connecticut Warbler	Max.	grid	-1.18	0.29	0.28	0.15	0.82	0.25
	Mean	grid	-0.64	0.35	0.74	0.19	1.06	0.31
Least Flycatcher	Max.	fixed only	-0.10	0.13	1.46	0.17	-	-
	Mean	grid	0.45	0.22	1.28	0.18	0.33	0.18
Mourning Warbler	Max.	grid	-0.28	0.10	0.08	0.09	0.22	0.10
	Mean	grid	-0.30	0.11	0.02	0.10	0.23	0.10
Ovenbird	Max.	fixed only	-0.43	0.08	0.40	0.12	-	-
	Mean	fixed only	-0.34	0.09	0.38	0.13	-	-
Rose-breasted Grosbeak	Max.	grid	-2.41	0.50	0.26	0.24	1.08	0.42
	Mean	grid	2.59	0.55	0.04	0.26	1.10	0.42
Red-breasted Nuthatch	Max.	grid	-1.22	0.25	0.34	0.17	0.58	0.22
	Mean	grid	-0.51	0.25	0.44	0.15	0.71	0.19
Red-eyed Vireo	Max.	grid	-0.41	0.13	0.17	0.11	0.39	0.10
	Mean	grid	-0.35	0.14	0.19	0.12	0.39	0.10
Western Tanager	Max.	grid	-1.97	0.34	0.02	0.22	0.68	0.29
	Mean	grid	-1.95	0.37	0.04	0.24	0.68	0.29
White-throated Sparrow	Max.	grid	0.22	0.12	0.21	0.10	0.39	0.10
	Mean	grid	0.28	0.11	0.17	0.11	0.39	0.10
Yellow-rumped Warbler	Max.	grid	-0.16	0.10	-0.13	0.11	0.26	0.09
	Mean	grid	-0.18	0.11	-0.09	0.12	0.26	0.09

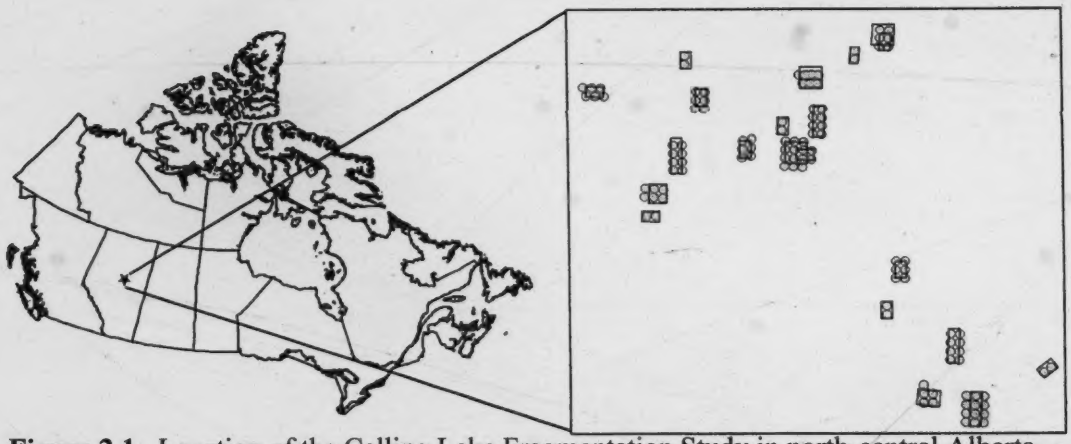

Figure 2.1. Location of the Calling Lake Fragmentation Study in north-central Alberta, dispersion of point-count stations also surveyed with spot-mapping and locations of spot-mapping grids.

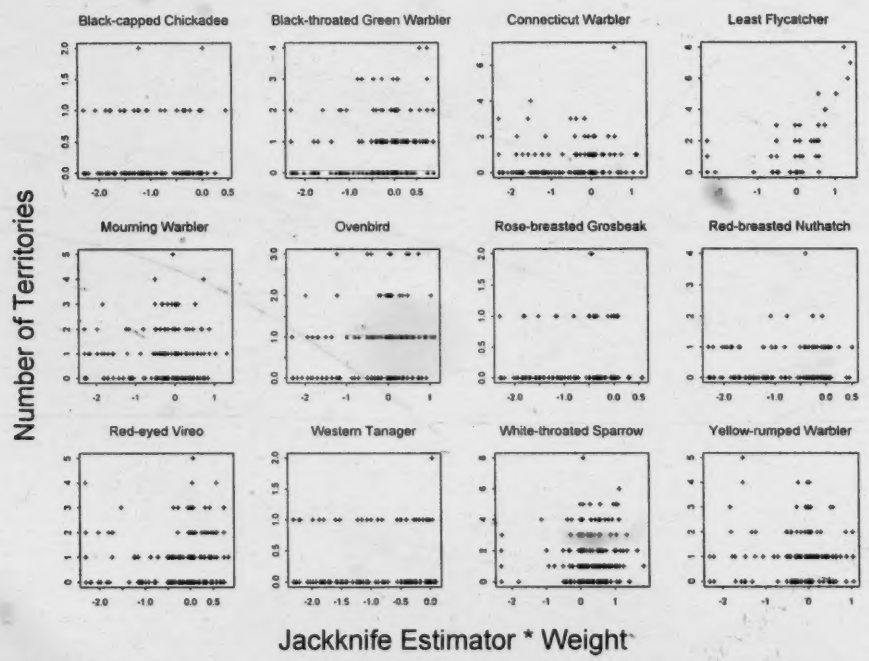

Figure 2.2. Relationship between the number of territories from spot mapping and the jackknife estimator of maximum point-count abundance, multiplied by sampling weights (proportion of point-count station overlapping spot-mapping grid). This is the relationship modelled. Plots of mean point-count abundance are similar (Appendix 1).

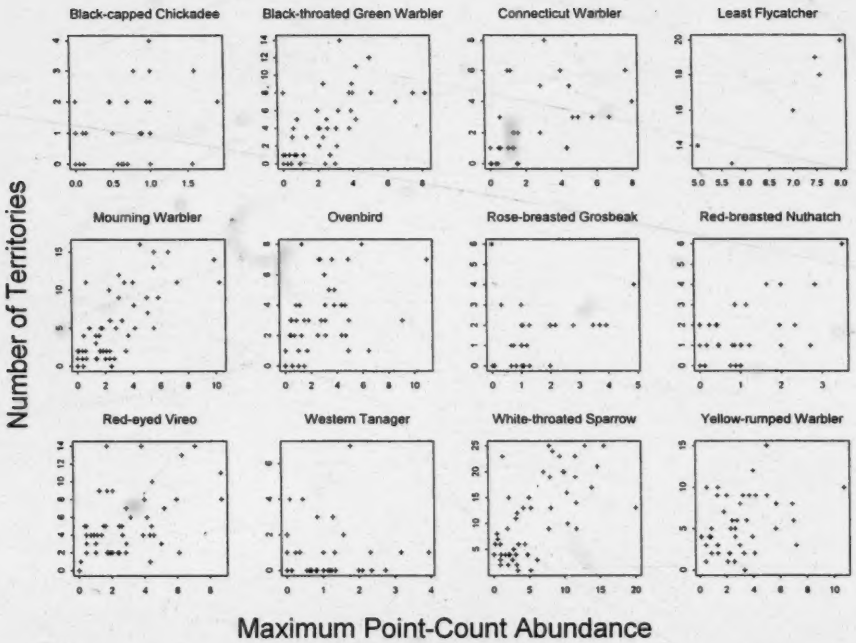

Figure 2.3. Relationship between number of territories in a spot-mapping grid and the maximum point-count abundance summed over all stations within that grid. Plots of mean point-count abundance are similar (Appendix 1).

Chapter 3: Finding appropriate spatial scales for studies of population dynamics in boreal songbirds.

Introduction

The main goal of population ecology is to characterize and understand changes in density of organisms over time and space. However, the patterns of abundance observed in any study depend on the spatial and temporal scale used for observation (Allen and Starr 1982, Carlile *et al.* 1989, Turner *et al.* 2001). Therefore, it is important to use spatial and temporal scales that are appropriate for the species being studied and the questions being asked. An appropriate temporal scale for studies of population dynamics is often suggested to be the length of a generation or breeding cycle (McArdle *et al.* 1990). However, choosing an appropriate spatial scale is more difficult.

Hierarchy theory states that organisms are influenced by processes occurring on several spatial and temporal scales, so that observed patterns of population dynamics and density differ depending on the scales of observation (Carlile *et al.* 1989, Sutcliffe *et al.* 1996, Turner *et al.* 2001). Suppose that a true underlying temporal pattern of population dynamics exists at some unknown spatial scale. If we observe these dynamics at a spatial scale smaller than appropriate, we might expect the true pattern to be confounded by the patchiness of habitats, interspecific competitive exclusion, sampling error and random variation (Sherry 1979, Thomas 1991, Qi & Wu 1996, Steen et al. 1996, Paradis et al. 2000). Similarly, if we observe them at a larger spatial scale than is appropriate, we would expect the true pattern to be obscured due to regional differences and reduced levels of dispersal (Carlile *et al.* 1989, Thomas 1991, Sutcliffe *et al.* 1996). Thus, we expect alternating patterns of asynchrony and synchrony in population dynamics as we increase the spatial scale of observation (Thomas 1991).

I suggest that appropriate spatial scales for studies of population dynamics in time are the range of spatial scales where the temporal dynamics are synchronous, i.e. the range of spatial scales where a single temporal pattern of population dynamics occurs. This ensures that the true underlying pattern of population dynamics is neither obscured due to

random variation nor to averaging multiple patterns of population dynamics, as described above. I term the smaller end of this range as the minimum extent of synchrony, and the larger end of the range the maximum extent of synchrony. Both measures are useful when designing surveys: the minimum extent of synchrony has been suggested as the optimal size of sample units (Greig-Smith 1952, Kershaw 1957, Mead 1974 and Carlile *et al.* 1989), and the maximum extent of synchrony can be used to ensure sampling units are spatially independent (Carlile *et al.* 1989, Lichstein *et al.* 2002). Here, I estimate minimum and maximum extents of synchrony for 25 songbird species found in the boreal mixedwood forest of North America.

The appropriate range of scales is expected to vary across species due to differences in life history characteristics or dispersal abilities of the organism (Paradis *et al.* 1999, Paradis *et al.* 2000). For example, appropriate spatial scales may be roughly proportional to the size of home ranges or to body size (Wiens 1989, Holling 1992, Roland and Taylor 1997). Larger species often have larger territories due to greater mobility and energy requirements (Holling 1992, Bowman *et al.* 2002). Wider spacing in a landscape may, in turn, result in larger spatial scales of synchrony within the population (Roland and Taylor 1997). However, Koenig (1998) found no relationship between body mass and extent of spatial autocorrelation, perhaps because territory sizes can differ widely for species with approximately equal body mass (e.g. Schoener 1968, Sherry and Holmes 1985). I predicted that both body mass and territory size would be positively correlated with minimum and maximum extents of synchrony.

Dispersal and Moran effects increase the degree and spatial extent of synchrony in population dynamics within and between populations. Moran effects are caused by external stochastic events, such as a severe storm, occurring simultaneously over a large spatial area. They increase synchrony by simultaneously affecting reproductive success or survival over a region, perturbing dynamics of unlinked populations in similar ways (Ranta *et al.* 1995, Steen *et al.* 1996, Watson *et al.* 2001). Dispersal increases synchrony by evening out areas with differential reproductive success or survival (Ranta *et al.* 1995, Steen *et al.* 1996). Juveniles of resident songbird species do not disperse as far from their natal site as do juveniles of migratory species, linking the dynamics of neighbouring areas more tightly (Paradis *et al.* 1998, Sutherland *et al.* 2000). Furthermore, external

stochastic events, such as storms or cold weather, would synchronize the same group of resident individuals year-round (Holmes and Sherry 2001). In contrast, individuals in breeding populations of migrant songbirds are thought to winter at different locations (Maurer and Villard 1994, Sillett *et al.* 2000), so that individuals within the breeding population are exposed to a different suite of external stochastic events. Therefore, I predicted that, on average, resident species would have more highly correlated temporal patterns of abundance, and be synchronized over larger minimum and maximum spatial extents of synchrony, than migratory species.

Thus, my main objective was to estimate the minimum and maximum extents of synchrony in population dynamics for 25 species in the boreal mixedwood forest. I also tested whether body mass, territory size and migratory guild were associated with the estimated spatial scales, as predicted above.

Methods

Study Areas

This study uses a subset of data from the Calling Lake Fragmentation Study (Schmiegelow *et al.* 1997, Schmiegelow & Hannon 1999), located in north-central Alberta, Canada (55°15' N, 113°35' W; Figure 3.1). The site encompasses approximately 14,000 ha of boreal mixedwood forest, dominated by old (80-130) aspen stands (*Populus tremuloides*). Some white spruce (*Picea glauca*) and black spruce (*Picea mariana*) are present. The Calling Lake Study includes experimentally fragmented blocks, but I used only data from undisturbed control blocks. Thus, point count stations were not evenly distributed across the study site (Figure 3.1). 93 stations were surveyed using point counts from 1993 through 2002 (Schmiegelow *et al.* 1997, Schmiegelow & Hannon 1999, Schmiegelow, unpublished data; Figure 3.1).

Birds were surveyed using 100m radius point counts located on a 200m grid (Schmiegelow *et. al.* 1997). Each station was surveyed for five minutes five times each breeding season (every ten days from the third week of May through late June). The first survey period was ignored in this study because most migrants were not yet breeding. I

estimated annual abundance at each point as the maximum number of individuals observed over the four survey periods, since I found the maximum abundance to be a better measure of territorial individuals than mean abundance (Chapter 2). More details of the sampling design are available in Schmiegelow *et. al.* (1997).

Data

I examined extent of synchrony in 25 species that were relatively abundant at one or both sites (Table 3.1). Information on body mass, territory size and migratory strategies for each species (Table 3.1) were obtained from the Birds of North America series (Morse 1993, Pitochelli 1993, Smith 1993, Briskie 1994, Falls and Kopachena 1994, Hall 1994, Van Horn and Donovan 1994, Moskoff and Robinson 1996, Dawson 1997, Pitochelli *et al.* 1997, Sherry and Holmes 1997, Hunt and Flaspohler 1998, James 1998, Middleton 1998, Rimmer and McFarland 1998, Ghalambor and Martin 1999, Hudon 1999, Lowther *et al.* 1999, Cimprich *et al.* 2000, Evans Mack and Yong 2000, Gardali and Ballard 2000, Hejl *et al.* 2002a, Hejl *et al.* 2002b, Walters *et al.* 2002, Wyatt and Francis 2002).

Minimum Extent of Synchrony

Before examining temporal patterns of abundance, I needed to determine the minimum and maximum spatial extent of synchrony in the population dynamics of each species. Adjacent point count stations may not have identical abundance estimates (e.g. due to random variation, habitat patchiness or territory placements offset from the sampling grid), even if the underlying distribution is consistent. This random or sampling variation will obscure trends in spatial autocorrelation of abundance patterns. Therefore, I determined the scale at which synchrony in temporal patterns of abundance was maximized.

Building on the work of Greig-Smith (1952), Kershaw (1957) and Mead (1974), I first clustered adjacent point count stations into groups of increasing sizes (e.g. individual point count stations, pairs of stations, four stations, etc.) and calculated the average correlation in temporal abundance patterns for adjacent clusters. However, correlations between averages will necessarily increase with the number of stations being averaged

(Wiegert 1962). Therefore, I used a randomization test to estimate the optimal cluster size for each species. For each run of the randomization test, I clustered random point count stations (instead of adjacent stations) and calculated the average correlation between "adjacent" clusters. Correlations resulting from 1000 runs were then tabulated, and used to determine the significance level of the average correlations observed. This value represents the probability that a correlation that large would be expected by randomly clustering plots, i.e. the probability that adjacent clusters are more highly correlated than clusters randomly selected from the study area. For each species, the cluster size with the most significant difference between the correlations observed and those expected under random clustering was then used as a measure of the minimum extent of synchrony.

Maximum Extent of Synchrony

I also needed to determine the maximum distance where a consistent temporal pattern of abundance, i.e. temporal population dynamics, occurred. To determine this maximum extent of synchrony, I examined the spatial autocorrelation in temporal abundance patterns. I plotted the correlations of temporal abundance patterns from all pairs of optimal clusters, as estimated above, as a function of distance between the clusters. If spatial autocorrelation exists, the correlation should decrease with increasing distance.

The spatial autocorrelation was quantified using a nonparametric technique, the spline correlogram (Bjørnstad and Falck 2001). This method uses a kernel smoother to estimate the pattern of spatial autocorrelation, rather than assuming any particular parametric function, and is asymptotically equivalent to the spatial Mantel correlogram (Bjørnstad and Falck 2001). The maximum extent of synchrony was defined as the distance where the correlation was no longer different from zero. This was estimated using 90% confidence interval bounds, a more conservative estimate than would result from the standard 95% confidence interval bound.

Covariates

I determined whether the minimum and maximum extents of synchrony were correlated with body mass, territory size and average correlation between neighbouring

point count stations. Data were not normal and could not be normalized with transformations. Therefore, Pearson's r^2 from linear regressions were used as a rough estimate of the strength of the relationships. Kruskal-Wallis rank sign tests were used to determine whether scales of synchrony were significantly different in species with different migratory strategies.

Results

The estimated minimum extents of synchrony comprised one or two 100m-radius point count stations for approximately half the species examined (13 of 25; Table 3.2). However, over a quarter of the species (7 of 25) had optimal cluster sizes of six point count stations, the largest minimum scale examined due to sample size constrictions. At these scales, the average correlation in population dynamics within a cluster ranged from 0.03 to 0.61. Population dynamics of most species were not more highly correlated within a cluster than would expected by randomly creating clusters at the site.

Estimates of maximum scale of synchrony were greater than or equal to the extent of the site, approximately 10km, for 14 of 25 species at Calling Lake (Table 3.2, Figure 3.2). This comprises all residents, short- and mid-distance migrants examined except Brown Creeper, but less than 50% of the long-distance migrants examined. Blue-headed Vireo, Red-breasted Nuthatch, Red-eyed Vireo, Tennessee Warbler and White-throated Sparrow were particularly strongly correlated, with significant correlations through 8km (where sample sizes become severely restricted).

Minimum and maximum scales exhibited only weak correlations with body mass (maximum extent $r^2=0.059$, minimum extent $r^2=0.020$), territory size (maximum extent $r^2=0.101$, minimum extent $r^2=0.011$) and average correlation of neighbouring stations (maximum extent $r^2=0.053$, minimum extent $r^2=0.115$). Moreover, the maximum and minimum extents did not differ between migratory guilds (maximum extent $p=0.173$, minimum extent $p=0.195$), although this test should be viewed with caution since most species were neotropical migrants.

Discussion

The appropriate spatial scale for any particular study depends on the questions and organisms being studied. Here, I demonstrated an approach that estimates appropriate spatial scales for examining population dynamics of a single species over multiple years. Most analyses of spatial autocorrelation in songbirds have examined similarities using a single data point at each location (e.g. Brown *et al.* 1995, Beard *et al.* 1999, Moskát 2000, Lichstein *et al.* 2002), although some have applied multivariate approaches (e.g. Koenig 1998, Koenig 2001). Single-year methods of estimating spatial autocorrelation in population dynamics are likely to provide less stable and representative estimates than multi-year methods.

Estimating the minimum extent of synchrony reduces the variation due to sampling with smaller than optimal units and thus improves estimates of the maximum extent of synchrony. The randomization procedure offers a way to select the best cluster size available. The p-values associated with this test should not be used as an indication of the strength of synchrony in population dynamics, however. The test compares the observed synchrony with that expected under a random distribution within the region or study site. Thus, if population dynamics are homogeneous across the entire study site, adjacent clusters may be only slightly more synchronous than clusters selected at random from within the site. Instead, the usual hypothesis tests for correlation should be used (i.e. using a Z-test for normally distributed data).

Koenig (1998, 2001), using multi-year approaches, found significant autocorrelation (maximum extents of synchrony) in abundance of some wintering songbird populations over very large distances (hundreds of kilometers), but not in others. There was no evidence for significant autocorrelation in abundance of breeding populations at the scales examined (but the first distance interval was 0-100km; Koenig 1998). Using single-year approaches, others have found significant correlations (i.e. maximum extents of synchrony) in abundance of breeding songbirds at a few hundred metres (Moskát 2000), a minimum of 3km (Lichstein *et al.* 2002) and over several hundred kilometers (Brown *et al.* 1995). My results are consistent with the variation seen previously; estimated maximum extents vary widely across species, with little or no spatial

autocorrelation for some species, but significant autocorrelation to a minimum of 10km for other species. Autocorrelation at these scales could result from dispersal or from external stochastic events synchronizing dynamics of neighbouring areas (Paradis *et al.* 1999, Paradis *et al.* 2000). The cause of the spatial autocorrelation is not addressed in this study.

Neither body mass nor territory size were significantly correlated with the scales of spatial autocorrelation, counter to what I predicted. However, there is some suggestion that neotropical migrants may, on average, be correlated over shorter distances than species in other migratory guilds: residents, short- and mid-distance migrants were more likely than neotropical migrants to be spatially autocorrelated at distances greater than or equal to 10km. However, some neotropical migratory species were significantly autocorrelated at this distance, so future work is necessary to determine whether differences between migratory guilds exist.

Given the limited area surveyed in this study, neither minimum nor maximum extents of synchrony could be estimated with certainty. It would be useful to conduct similar analysis with stations scattered over a larger spatial extent and with larger groups of stations to improve the estimates of minimum and maximum extents of synchrony for these species. Nevertheless, based on these and previous results, the appropriate spatial scale for examining temporal changes in abundance seems to be species-specific. Unfortunately, there does not appear to be any obvious way of accurately predicting these scales a priori.

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Table 3.1. Natural history parameters used as covariates. All values were obtained from the Birds of North America series (see *Data* for references).

Species	Migration Strategy[1]	Body Mass (g)	Territory Size (ha)
American Redstart (*Setophaga ruticilla*)	LD	8.6	0.7
Black-capped Chickadee (*Poecile atricapillus*)	R	12.0	3.4
Black-throated Green Warbler (*Dendroica virens*)	LD	9.0	0.5
Blue-headed Vireo (*Vireo solitarius*)	LD	15.3	3.0
Brown Creeper (*Certhia americana*)	SD	8.4	4.3
Chipping Sparrow (*Spizella passerina*)	MD	13.2	0.6
Connecticut Warbler (*Oporornis agilis*)	LD	15.3	0.4
Least Flycatcher (*Empidonax minimus*)	LD	10.5	0.1
Magnolia Warbler (*Dendroica magnolia*)	LD	8.6	0.7
Mourning Warbler (*Oporornis philadelphia*)	LD	12.3	0.7
Ovenbird (*Seiurus aurocapillus*)	LD	22.1	1.0
Philadelphia Vireo (*Vireo philadelphicus*)	LD	12.2	0.6
Pine Siskin (*Carduelus pinus*)	R	12.9	colonial
Red-breasted Nuthatch (*Sitta canadensis*)	R	10.5	5.1
Red-eyed Vireo (*Vireo olivaceus*)	LD	20.4	0.7
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	LD	46.4	0.8
Swainson's Thrush (*Catharus ustulatus*)	LD	29.8	1.5
Tennessee Warbler (*Vermivora peregrina*)	LD	9.4	N/A
Warbling Vireo (*Vireo gilvus*)	LD	11.9	1.5
Western Tanager (*Piranga ludoviciana*)	LD	30.0	2.8
White-throated Sparrow (*Zonotrichia albicollis*)	SD	25.2	1.0
Winter Wren (*Troglodytes troglodytes*)	SD	9.1	2.4
Yellow-bellied Sapsucker (*Sphyrapicus varius*)	LD	50.3	2.0
Yellow-rumped Warbler (*Dendroica coronata*)	LD	12.6	0.6
Yellow Warbler (*Dendroica petechia*)	LD	9.8	0.3

[1] Migration: **R** resident, **SD** short distance (northern US), **MD** moderate distance (southern US, Mexico), **LD** long distance (central America, Caribbean, South America)

Table 3.2. Estimated minimum and maximum extents of synchrony at Calling Lake.

	Minimum Extent			Maximum Extent	
Species	Cluster Size	Corr. (r)	p-value	Estimate	Lower CI
American Redstart	1	0.08	0.20	2.0	1.2
Black-capped Chickadee	2	0.19	0.10	>10.0	6.5
Black-throated Green Warbler	2	0.03	0.75	4.6	3.1
Blue-headed Vireo	1	0.09	0.20	>10.0	8.7
Brown Creeper	6	0.18	0.28	0.0	0.0
Chipping Sparrow	6	0.25	0.55	>10.0	4.2
Connecticut Warbler	5	0.23	0.45	>10.0	0.0
Least Flycatcher	1	0.11	0.40	9.6	3.3
Magnolia Warbler	6	0.24	0.10	4.6	0.0
Mourning Warbler	3	0.22	0.02	>10.0	2.8
Ovenbird	6	0.56	0.01	>10.0	6.0
Philadelphia Vireo	2	0.10	0.25	6.1	0.0
Pine Siskin	2	0.21	0.30	>10.0	0.0
Red-breasted Nuthatch	1	0.31	0.01	>10.0	>10.0
Red-eyed Vireo	1	0.14	0.15	>10.0	>10.0
Rose-breasted Grosbeak	2	0.28	<0.01	>10.0	1.5
Swainson's Thrush	4	0.15	0.30	5.1	0.0
Tennessee Warbler	1	0.61	0.17	>10.0	>10.0
Warbling Vireo	3	0.19	0.02	6.7	0.0
Western Tanager	4	0.11	0.35	6.0	0.0
White-throated Sparrow	2	0.43	0.31	>10.0	8.6
Winter Wren	6	0.49	0.30	>10.0	7.4
Yellow-bellied Sapsucker	2	0.18	0.05	>10.0	2.3
Yellow-rumped Warbler	6	0.27	0.15	2.2	0.0
Yellow Warbler	6	0.48	0.05	2.4	1.6

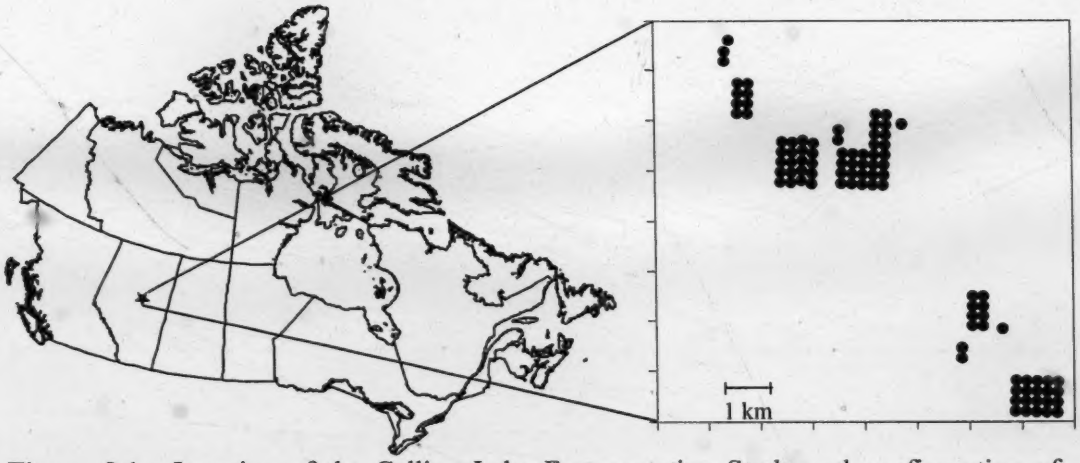

Figure 3.1. Location of the Calling Lake Fragmentation Study and configuration of control point count stations.

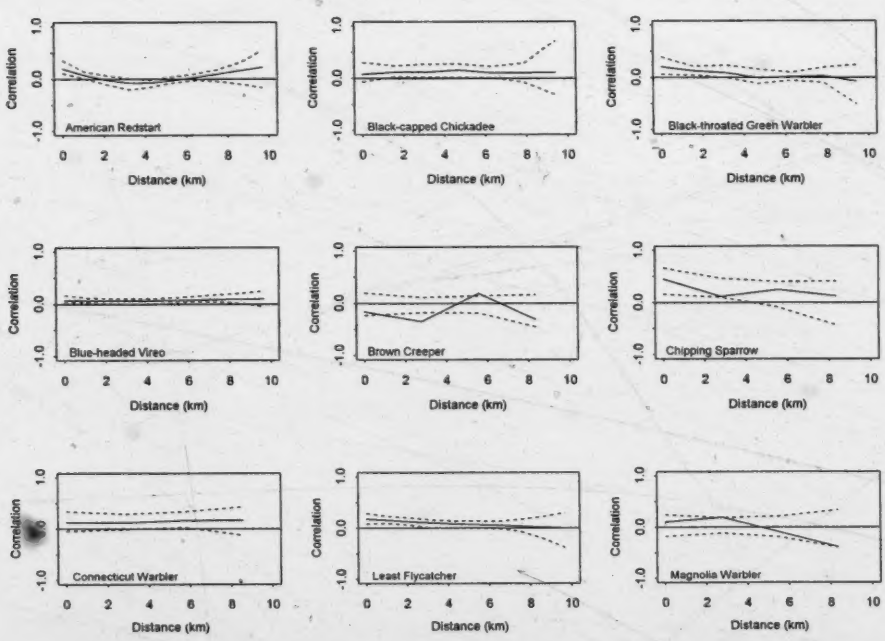

Figure 3.2. Spatial autocorrelation of temporal patterns of population dynamics (10 years) for 25 species at Calling Lake used to estimate maximum extents of synchrony. Solid lines are estimates, dotted lines are 90% confidence intervals.

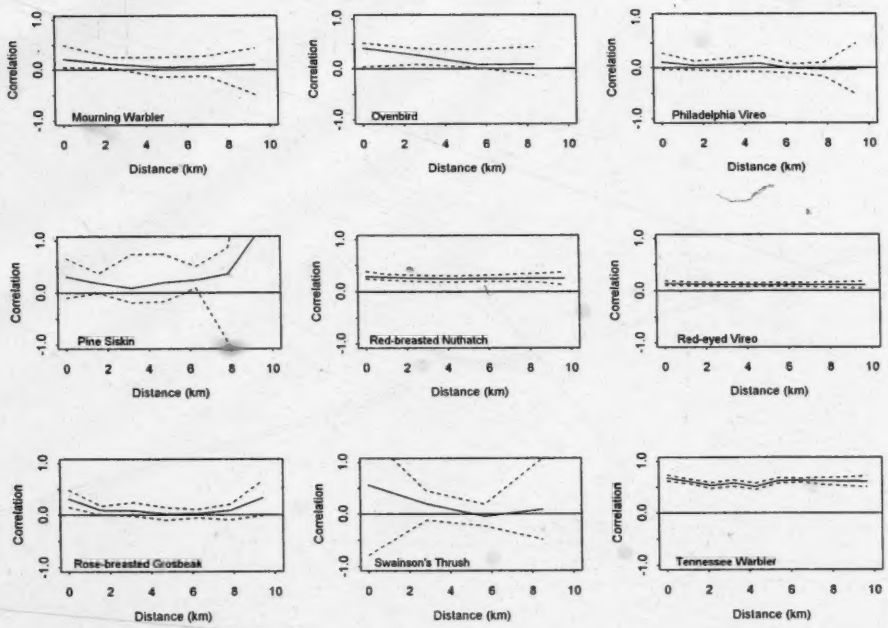

Figure 3.2 cont…

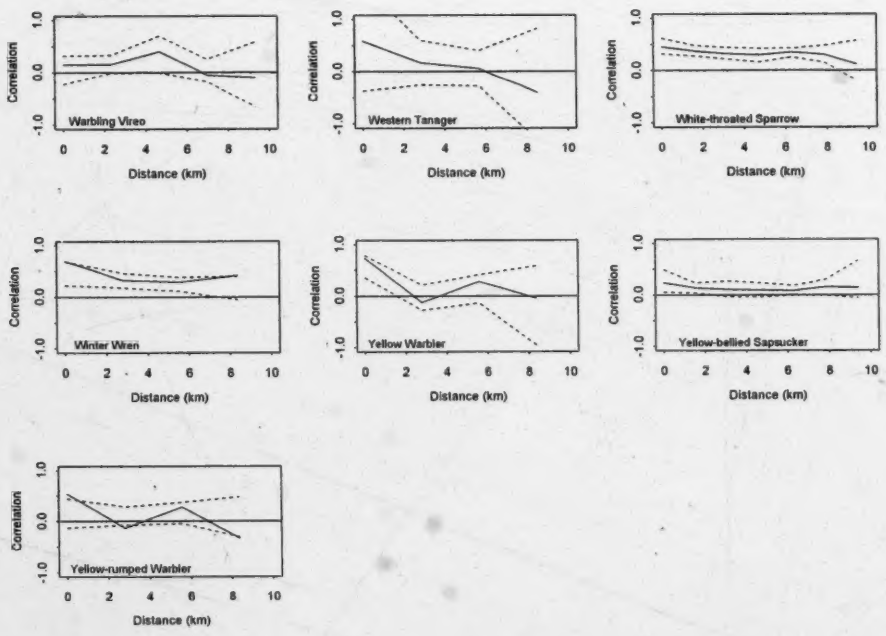

Figure 3.2 cont…

Chapter 4: A search for factors that spatially synchronize population dynamics of boreal songbirds.

Introduction

The degree of spatial synchrony in the population dynamics of a species can influence its population persistence both positively and negatively. Asynchrony in population dynamics is a critical component of metapopulation theory; some asynchrony in dynamics of sub-populations can increase the persistence of the super-population even when individual sub-populations are extirpated (Heino *et al.* 1997). Conversely, synchrony in population dynamics over large spatial scales is often seen in trees. Mast flowering and fruiting events, when most individuals within a region flower synchronously, are thought to be an adaptation to increase wind-pollination success or reduce predation of seeds (Kelly 1994, Kelly *et al.* 2001), thereby increasing population persistence.

Spatial synchrony in population dynamics may occur because of dispersal and Moran effects. Moran effects occur when stochastic events that perturb reproductive success or survival, such as a severe storm, occur over a large area (Ranta *et al.* 1995, Ranta *et al.* 1999). As long as the density-dependent structure of the two population units is reasonably similar, Moran effects can synchronize their population dynamics (Hudson and Cattadori 1999). Dispersal links population units, so that large fluctuations in density at one location affect a broader spatial extent. This increases spatial synchrony in population dynamics, with synchrony decreasing as the distance between locations increases and the rate of dispersal decreases (Ranta *et al.* 1995, Ranta *et al.* 1999). Both mechanisms have been shown to synchronize population dynamics of birds (e.g. Paradis *et al.* 1999, Watson *et al.* 2000). In Chapter 3, I found 15 boreal songbird species whose population dynamics appeared to be synchronous over areas larger than 100km^2. Here, I attempted to identify whether dispersal, Moran effects, or both are probable mechanisms leading to this spatial synchrony.

I used an indirect approach to identify plausible causes of synchrony in the population dynamics of these species, modelling the abundance of each species as a function of factors postulated to influence abundance by dispersal into the area from the surrounding landscape or by Moran effects. Two factors, abundance of Lepidopteran larvae and area burnt by forest fires, were postulated to affect bird population dynamics by affecting recruitment into the population from the surrounding landscape (no insect outbreaks or fires occurred within the study area during this period). For example, spruce budworm outbreaks are associated with numerical responses and increases in fecundity in several species (MacArthur 1958, Morris *et al.* 1958, Zach and Falls 1975). All species in this study regularly include Lepidopteran larvae in their diet during the breeding season. They are also largely forest-dependent, so fires may reduce the amount of suitable habitat available on the landscape, depending on the fire severity.

The other factors examined were expected to be relatively constant over large areas, and were postulated to influence population dynamics through Moran-type effects. Cone crops may be an important winter food source for several species (Black-capped Chickadee *Poecile atricapillus*, Pine Siskin *Carduelis pinus* and Red-breasted Nuthatch *Sitta canadensis*), and are known to be autocorrelated over large distances (e.g. a minimum of 500km for white spruce *Picea glauca*; Koenig and Knops 1998, 2000). White spruce is the only species in this region that has irregular cone crops, and has enough commercial value for the crop to be measured in any way. Kemp and Keith (1970) showed that white spruce cone crops are fairly synchronous in Alberta. Furthermore, evidence from other species suggests that the proportion of filled seed (i.e. seeds with nutritive value) may be higher in years with larger crops (Eastham and Jull 1999, Houle 1999). Thus, the net availability of white spruce seed during the winter will vary widely between years, potentially influencing over-winter survival.

Weather during the breeding and wintering seasons may also influence population dynamics of songbirds (e.g. Zumeta and Holmes 1978, Thompson *et al.* 1997) and is correlated over large spatial scales (Kiladis and Diaz 1989). During the breeding season, unusually cold or wet weather, particularly in combination, could lower reproductive success by reducing foraging efficiency and increasing the time adults need to spend away from the nest (Dawson 1997, Walters *et al.* 2002).

Species that are resident in Alberta have to cope with extreme cold (e.g. mean daily temperatures to -40°C). Obviously, such temperatures in combination with reduced foraging opportunities due to shorter day-lengths can impact survival, particularly if extreme conditions persist for several days (Smith 1991). It is more difficult to determine an appropriate measure of winter weather for migrants, largely because we don't know which part of their wintering range the breeding populations of Alberta use. As a proxy, I used the Southern Oscillation Index (SOI), a measure of the El Niño/ La Niña phenomenon that strongly influences weather patterns in northern South America, Central America and the southern United States (Mauget and Upchurch 1999, Wright *et al.* 1999), where neotropical migrants typically winter. Large negative values of this index represent El Niño conditions; large positive values represent La Niña conditions. The expected impact of El Niño and La Niña events on the population dynamics of migratory species depends on where they over-winter, and will be deferred to the discussion.

Finally, I also investigated whether the phenology of flowering trees and shrubs was important using the spring flowering index of Beaubien and Freeland (2000). This index is the mean first bloom date for *Populus tremuloides* (aspen), *Amelancher alnifolia* (saskatoon) and *Prunus virginiana* (chokecherry), species that are common within the study region. Phenology was expected to be more important for long-distance migrants than for residents or short-distance migrants, because they are more susceptible to cold weather and have a more limited time in which to breed (e.g. Least Flycatcher *Empidonax minimus*, Briskie 1994). If most individuals normally breed at the study site, but chose to stop at more southerly sites in years with late springs then abundance would be negatively correlated with phenology. Alternately, the correlation could be positive if most individuals usually breed farther north, but chose to stop at the study site in years with late springs. Thus, phenology may desynchronize population dynamics by reducing site fidelity and mixing breeding populations.

Methods

Study Areas

This study uses a subset of data from the Calling Lake Fragmentation Study (Schmiegelow *et al.* 1997; Schmiegelow & Hannon 1999), located in north-central Alberta, Canada (55°15' N, 113°35' W; Figure 4.1). The site encompasses approximately 14,000 ha of boreal mixedwood forest, dominated by old (80-130) aspen stands. Some white spruce and black spruce (*Picea mariana*) are present. The Calling Lake Study includes experimentally fragmented blocks but I used only data from undisturbed control blocks. Thus, point count stations were not evenly distributed across the study site. 93 stations were surveyed using point counts from 1993 through 2002 (Schmiegelow *et al.* 1997; Schmiegelow & Hannon 1999, Schmiegelow, unpublished data).

During the Calling Lake point count surveys, 100m radius plots were located on a 200m grid (Schmiegelow *et. al.* 1997). A standard five-minute count protocol was used. Each station was surveyed 5 times each breeding season (every ten days from the third week of May through late June). The first survey period was ignored in this study because most migrants were not yet breeding. I chose to estimate annual abundance at each point as the maximum number of individuals observed over the remaining four survey periods, since I found maximum abundance to be a better measure of territorial individuals than mean abundance (Chapter 2). More details of the sampling design are available in Schmiegelow *et. al.* (1997).

To determine whether the population dynamics at Calling Lake were similar to those in other areas, I compared them with point count data collected near Meanook, Alberta (Hannon 1993 and unpublished data), located approximately 70 km south of the Calling Lake site (54°37' N, 113°20' W; Figure 4.1), in an agricultural landscape. Forest was similar in age and species composition to Calling Lake. Seven point count stations were surveyed annually from 1990-2002 in a 140ha block of forest. An additional four stations were surveyed for three or four consecutive years within this period. All point counts were conducted in forest. More details of the sampling design are available in Hannon (1993).

At Meanook, point count surveys used unlimited distance plots, so I removed all observations in the "very far" distance class (roughly, distances greater than or equal to 200m). Points were surveyed for six minutes over four rounds at roughly two-three week intervals from the second week of May through the end of June. Annual abundance at each point was estimated as the maximum number of individuals observed over the four survey periods.

Data

I examined 15 species that were relatively abundant at one or both sites and had population dynamics that were synchronous over the extent of each study site (Chapter 3, Appendix 3): Black-capped Chickadee, Blue-headed Vireo (*Vireo solitarius*), Chipping Sparrow (*Spizella passerina*), Connecticut Warbler (*Oporornis agilis*), Least Flycatcher, Mourning Warbler (*Oporornis philadelphia*), Ovenbird (*Seiurus aurocapillus*), Pine Siskin, Red-breasted Nuthatch, Red-eyed Vireo (*Vireo olivaceus*), Rose-breasted Grosbeak (*Pheucticus ludovicianus*), Tennessee Warbler (*Vermivora peregrina*), White-throated Sparrow (*Zonotrichia albicollis*), Winter Wren (*Troglodytes troglodytes*) and Yellow-bellied Sapsucker (*Sphyrapicus varius*). Information on migratory strategies and diet of each species were obtained from the Birds of North America series (Pitochelli 1993, Smith 1993, Briskie 1994, Falls and Kopachena 1994, Van Horn and Donovan 1994, Dawson 1997, Pitochelli *et al.* 1997, James 1998, Middleton 1998, Rimmer and McFarland 1998, Ghalambor and Martin 1999, Cimprich *et al.* 2000, Hejl *et al.* 2002, Walters *et al.* 2002, Wyatt and Francis 2002).

Spatial Scales

In Chapter 3, I determined that population dynamics of the 15 species at Calling Lake were synchronous to distances ≥ 8km. Similar analyses were conducted to determine whether these scales were appropriate at Meanook (Appendix 3). As far as could be determined with the limited extent of the Meanook site, results suggest that patterns of spatial autocorrelation are roughly comparable at the two sites. Thus, temporal patterns of abundance at both sites were extracted at spatial scales determined to be appropriate for Calling Lake data.

I also showed that point counts are consistent estimators of the number of territorial individuals, and that differences in point count abundance correspond linearly to differences in density (Chapter 2). Thus, time series of relative population abundance are equivalent to time series of true densities. Time series were extracted by a two-stage process: (1) averaging all point count stations within clusters corresponding to the minimum scale; (2) averaging all clusters within a region corresponding to the maximum scale (Figure 4.2; see Chapter 3).

Covariates

An appropriate spatial scale for examining fires and insect outbreaks might be in the region delineated by natal dispersal distance, the distance between a natal site and the site of first breeding. Unfortunately, dispersal distances are poorly known for most songbird species. I found estimates of natal dispersal distances for only three of the species examined here; maximum known distances of dispersal are 39 km for Black-capped Chickadee (Desrochers *et al.* 1988), 53km for Winter Wren (Hejl *et al.* 2002) and 80km for Rose-breasted Grosbeak (Wyatt and Francis 2002). Dispersal distances are probably underestimated for most species, given their highly skewed distributions (Paradis *et al.* 1998) and the limited extent of study areas. Therefore 80km might be considered a conservative approximation to the distance where dispersal could link populations.

Data on spatial location and extent of forest fires were obtained from the Alberta Provincial Government (Department of Sustainable Resource Development, Forest Protection Division). Fires were postulated to influence songbird population dynamics through recruitment of juveniles and adults displaced from former territories. In this circumstance, adults could easily disperse farther than is typical for breeding dispersal (dispersal between breeding sites, which is usually less than natal dispersal distances; Greenwood 1980, Paradis *et al.* 1998). Thus, an index of fire prevalence was calculated as the total area burnt during the previous year within 80km of the site midpoint (Figure 4.3). There were many years with no fires within this region, and two years with relatively large areas burnt; therefore, I $\log_{10}$ transformed the data to reduce the influence of those two years on the regression, adding 1 ha to all years to deal with the zeros.

Information on spatial location and extent of insect outbreaks was derived from aerial surveys carried out by the Alberta Provincial Government (Department of Sustainable Resource Development, Forest Health Division) for forest pest species. These surveys map the extent of moderate or severe insect defoliation within the managed forest regions of the province. Because the mapped areas represent only areas with significant tree defoliation, elevated insect populations will be present in areas not represented on the map. In particular, insect populations may be elevated some distance beyond the mapped areas. Incidence of forest tent caterpillar (*Malacosoma disstria*) cocoons drops off rapidly within a few kilometers of the mapped regions (J. Roland, personal communication), but spruce budworm are spatially autocorrelated over greater extents than forest tent caterpillars (Peltonen *et al.* 2002). Therefore, I assumed that, on average, insect populations were elevated in a region 20km beyond the mapped areas. Unfortunately, data for aspen defoliators is currently available only for 1998-2002, so analyses were limited to examining the effect of a conifer defoliator, spruce budworm (*Choristoneura fumiferana*). Thus, an index of spruce budworm abundance was derived as follows: total area defoliated by spruce budworm within 100km of the site midpoint during the previous year. Spruce budworm outbreaks were included in analyses only for Calling Lake because they occurred within 100km of Meanook only during 1997 (Figure 4.3).

Peters (2003) showed that the volume of white spruce cones collected in Alberta each year was correlated with cone abundance measured at several sites in northern Alberta, and with an index of red squirrel (*Tamiasciurus hudsonicus*) abundance. In particular, the volume of cones collected was effective at identifying years with large cone crops. It is also correlated with measurements of seed rain taken near Calling Lake for 1993-1996 (Stewart *et al.* 2000). Thus, the volume of white spruce cones collected in Alberta during the previous autumn was used as an index of cone crop abundance for a given year (Figure 4.3).

Daily weather data from the Calling Lake weather station (55.21N, 113.2W) was obtained from the Alberta Provincial Government (Environment Department, Land and Services Division). This was the closest weather station to both study sites (Calling Lake and Meanook). I defined the breeding season as April through June for resident species,

and May through July 15 for migratory species. Defining unusually cold or wet weather is difficult. I based my criteria on a storm event known to have severely impacted songbird reproductive success at the Meanook study site (S. Hannon, personal observation), and strongly suspected to have similarly impacted reproductive success at the Calling Lake study site (T. Morcos, personal observation), during the summer of 2003. This storm event was not associated with extremely cold temperatures (mean temperatures ranged between 7° and 10°C), but was associated with one day of very heavy rain (> 45mm) and two more days with >15mm rain. Single days of heavy rain associated with somewhat higher temperatures did not similarly impact reproductive success. Similar conditions in New England have resulted in the death of many Scarlet Tanagers (*Piranga olivacea*; Zumeta and Holmes 1978). Therefore, I chose to define "bad" weather for migrants as temperature <10°C and total precipitation >10mm in a given day and construct the index to adjust for the length of the weather event. Acclimation can significantly increase tolerance to lower temperature (Chaffee and Roberts 1971, Calder and King 1974, Dawson and Whitlow 2000) and resident species have well-insulated nests (Smith 1993, Dawson 1997, Ghalambor and Martin 1999). Nevertheless, freezing temperatures might increase the cost of incubating eggs by 25% in Black-capped Chickadees (Smith 1991) and snow can increase the costs of foraging (Dawson 1997, Dolby and Grubb 1999). I thus defined "bad" weather for residents as temperatures <0°C and total precipitation >10mm. The severity of the breeding season was coded as 1 if no days of bad weather were observed, 2 if one or two 1-3 day periods of bad weather were observed, and 3 if one or more ≥4 day periods of bad weather were observed. Breeding season weather was expected to impact reproductive success and survival of adults, and thus was included in models with a one-year lag (Figure 4.3).

I defined winter as November through February. Brittingham and Temple (1988) used -18°C as a critical temperature in a study of Black-capped Chickadees in Wisconsin. I assumed that acclimation might allow residents in Alberta to cope with somewhat harsher temperatures (Chaffee and Roberts 1971, Calder and King 1974, Dawson and Whitlow 2000), and chose to use -25°C as a critical temperature. Thus, I created an index of winter severity by summing the following weights for cold periods: 1-3 day periods were assigned a weight of 0.5, 4-7 day periods had a weight of 1.0, 8-11 day

periods had a weight of 2.0 and ≥12 day periods had a weight of 3.0. Winter weather was only modelled for resident species (Black-capped Chickadees, Pine Siskin and Red-breasted Nuthatch; Figure 4.3), and was modelled with a half-year lag (i.e. weather in the winter of 2000-2001 would be associated with 2001 bird abundances).

Values of the SOI were obtained from the National Oceanic and Atmospheric Administration (National Weather Service, Climate Prediction Centre). I averaged the standardized values for November through February of the previous winter. Values for the spring flowering index of phenology were obtained from Beaubien and Freeland (2000) and unpublished data for 1997-1999 (Beaubien, personal communication). Unfortunately, values for 2000-2002 were not available (Figure 4.3).

Individual multiple linear regression models were constructed for each site and species. The dependent variable was an average of counts, so models based on normal distributions were appropriate. Since phenology data were not available for 2000-2002, this factor was excluded for models using all available bird data. Another set of models including phenology was run excluding 2000-2002 bird data. Since the analyses were meant to be exploratory and the timeseries were relatively short, backwards stepwise regression was used to identify models with minimal subsets of factors and a significance level of $p=0.10$ was used to identify factors of potential interest. Finally, since nest predation by squirrels and nest parasitism by Brown-headed Cowbirds are known to impact reproductive success of songbirds, I also investigated whether residuals from the regressions were correlated with the number of red squirrels or Brown-headed Cowbirds (*Molothrus ater*) seen or heard during point counts of songbirds in the previous summer (Figure 4.3). Since five-minute point-counts are not a very effective method of surveying for these species (Rothstein *et al.* 2000, N. Darlow, personal communication) and could be unreliable, I chose to exclude them from the regression models and take this more exploratory approach. I used a multiple comparison error rate of 0.10 for each site-model combination, such that p-values ≤ 0.015 for individual tests were considered significant. All analyses were conducted with S-Plus 4.5.

Results

Results of the regression models were mixed. At both sites, population dynamics of some species were not correlated with any of the factors examined (Table 4.1). However, most models found that one or more factors explained a significant portion of the changes in abundance. Many species were correlated both with factors hypothesized to act through dispersal (spruce budworm abundance and prevalence of fire) and those hypothesized to act through Moran effects (breeding weather, winter weather and SOI), but cone crops were never significantly correlated with population dynamics. Phenology was often positively correlated with abundance, particularly at Meanook, but was also negatively correlated for some species (Table 4.1). In contrast to my expectations, Black-capped Chickadees at Meanook were positively correlated with the severity of breeding season weather. Population dynamics of many species were negatively correlated with fire at Calling Lake, but positively correlated at Meanook (excepting White-throated Sparrow; Table 4.1). The SOI was positively correlated with abundance of some species, but negatively correlated with the abundance of other species.

Residuals from regressions of Least Flycatcher abundance were negatively correlated with the number of red squirrels observed during point counts for the 1993-2002 Calling Lake model (individual p-value=0.001; Table 4.2), and positively correlated with the number of Brown-headed Cowbirds observed for all models except 1993-1999 Calling Lake (individual p-values=0.01; Table 4.3). Residuals for Ovenbirds in the 1993-1999 Calling Lake model were significantly negatively correlated with observations of Brown-headed Cowbirds (p=0.01; Table 4.3). No other significant correlations were observed.

Discussion

This study attempted to identify potential mechanisms driving the observed spatial synchrony in population dynamics of 15 songbird species. As this study is correlative and timeseries are relatively short (10-12 years), the results should be treated as tentative. The inconsistency of results between the two sites may reflect the short timeseries used.

Nevertheless, I feel this study identifies some of the factors that may be important in driving population dynamics of these species on regional scales.

Dispersal-mediated Effects

Fire is considered to be the major natural disturbance affecting the composition and structure of boreal mixedwood forests, and I found eight species that seemed to respond to fires on a landscape scale. Four species (Blue-headed Vireo, Ovenbird, Rose-breasted Grosbeak and Red-eyed Vireo) were positively correlated with the area burnt in the landscape surrounding Meanook during the previous summer. Movement of adults into unaffected portions of logged landscapes at local scales has previously been documented (Schmiegelow *et al.* 1997); similar movements of adults and possibly juveniles (depending on the timing of the fire) could be occurring here on larger scales. Six species (Blue-headed Vireo, Chipping Sparrow, Connecticut Warbler, Red-eyed Vireo, White-throated Sparrow and Yellow-bellied Sapsucker) were more abundant at Calling Lake when less of the surrounding landscape was burnt the previous summer; however, White-throated Sparrows were less abundant at Meanook when less of the surrounding landscape was burnt the previous summer. White-throated Sparrows prefer forest edges and other relatively open, shrubby habitats (Falls and Kopachena 1994), and are found at high densities in residual patches within recently burnt landscapes (Schieck and Hobson 2000). Thus, White-throated Sparrows may preferentially disperse into recently burnt habitats from the study areas. However, the response of the other species was unexpected because none of the fires occurred at the site itself. Although these species are not found at high densities in recently burnt areas (Schieck and Hobson 2000), they tend to prefer forest edges and shrubbier habitats that may be found in the larger residual patches within burnt landscapes (Pitochelli *et al.* 1997, James 1998, Middleton 1998, Cimprich *et al.* 2000, Walters *et al.* 2002). Blue-headed and Red-eyed Vireos responded differently at the two sites. Meanook is located in an agriculturally fragmented landscape, while the landscape surrounding Calling Lake comprises forested stands of all ages. Suitable habitat for these species may be restricted at Meanook, forcing displaced individuals to settle in forested fragments. Alternatively, there may have been differences in the severity of fires in the areas surrounding the two sites.

Insect outbreaks are another factor influencing the forest dynamics of this region. Three species, Blue-headed Vireo, Connecticut Warbler and Red-eyed Vireo, were more abundant in the year following spruce budworm outbreaks, presumably due to an increase in the numbers of juveniles dispersing from these areas. Although Red-eyed Vireo are known to respond to outbreaks of other Lepidoptera (Holmes *et al.* 1986), Morris *et al.* (1958) found no response of Blue-headed Vireo to a spruce budworm outbreak. Interestingly, Tennessee Warblers are known spruce budworm specialists (Rimmer and McFarland 1998) but were not significantly correlated with the area defoliated. Tennessee Warbler densities tend to be higher during spruce budworm outbreaks (Rimmer and McFarland 1998), so there may have been room for juveniles to set up territories in the outbreak area rather than dispersing to our study sites. Moreover, Tennessee Warblers may be more vagile than non-specialist species, based on relatively low site fidelity (Rimmer and McFarland 1998). If so, the spatial scale used to extract the insect information may not have been appropriate for this species.

Moran Effects

Given the importance of cone crops for resident songbirds during the winter, fluctuating cone crops were expected to be an important mechanism acting to synchronize population dynamics. Surprisingly, they did not appear to be important for any of the residents examined. Several studies have shown that eruptions of residents to wintering areas south of their normal range are caused by failure of cone crops (Bock and Lepthien 1976, Koenig and Knops 2001). Perhaps this adaptive strategy of erupting during food shortages prevents the decrease in over-winter survival that would otherwise result. Lack of correlation between abundance and seed crops was also noted by Wesołowski and Tomiałojć (1997) for European seed-eating residents.

Weather was expected to synchronize population dynamics through Moran effects, i.e. by perturbing them in the same way over large spatial scales. In fact, eight species (over half those studied) were correlated with one or more measure of weather: winter season severity (modelled for residents only), breeding season severity and the SOI (Southern Oscillation Index). Only the Black-capped Chickadee was significantly correlated with my index of winter weather severity. Although thermal limits are lower

in species with larger body mass (Calder and King 1974, Dawson and Whitlow 2000), Black-capped Chickadees are approximately the same body mass as Red-breasted Nuthatches and Pine Siskins. Differences in foraging behaviour and location, however, could increase the sensitivity of Chickadees to cold weather (e.g. Dolby and Grubb 1999, Brotons *et al.* 2001).

Weather during the breeding season should also be important, since the energetic costs of incubating a nest or foraging during inclement weather are increased (Calder and King 1974, Smith 1991, Dawson 1997). Four species, Blue-headed Vireo, Connecticut Warbler, White-throated Sparrow and Yellow-bellied Sapsucker, were less abundant in years following cold summers. Yellow-bellied Sapsuckers may have difficulty foraging in years with cold weather if sap flow in trees is reduced, and egg mortality is known to increase during extended periods of cold weather (Walters *et al.* 2002). However, there is no obvious reason why the other three migrants would be particularly susceptible to cold weather in the breeding season. Unexpectedly, I found that Black-capped Chickadees at Meanook were more abundant the year after a cold summer. Lower reproductive success in cold summers would result in at best no effect, even if my measure of severe weather was poorly constructed. Although this result could be spurious, I propose an alternate hypothesis. Cresswell and McCleery (2003) found that Great Tits (*Parus major*) had larger clutch sizes in cold years, apparently as a consequence of delaying the start of incubation, and Perrins (1979) noted that female tits that have begun laying will continue during a cold spell. Furthermore, clutch size was positively correlated with juvenile survival to the following year in Willow Tits (*Parus montanus*; Eckman and Askenmo 1986). If Black-capped Chickadees can successfully raise larger than normal clutches resulting from cold spells during laying, more yearlings might enter the population following such years.

The Southern Oscillation Index (SOI) was correlated with survival and fecundity of Black-throated Blue Warblers wintering in Jamaica (*Dendroica caerulescens*; Sillett *et al.* 2000) and with reproductive success of several songbirds in the Pacific Northwest (Nott *et al.* 2002). Here, I found that the SOI was positively correlated with abundance of Black-capped Chickadee, Chipping Sparrow, Connecticut Warbler, Red-eyed Vireo and Tennessee Warbler, but negatively correlated with abundance of Blue-headed Vireo.

Tennessee Warblers winter in Central America and northern South America (Rimmer and McFarland 1998), while Connecticut Warblers and Red-eyed Vireos winter in northern South America (Cimprich *et al.* 2000). In these regions, El Niño events (negative SOI values) are associated with droughts (Wright *et al.* 1999). Blue-headed Vireos have part of their wintering range in Central America, but are mostly found along the northern Gulf of Mexico coast (James 1998). Here, La Niña events (high SOI values) are associated with hot, dry weather (Mauget and Upchurch 1999) which may negatively influence the abundance of the insects and fruit they eat in winter (James 1998). Chipping Sparrow winter in Mexico and throughout the southern United States (Middleton 1998). Thus, I might expect them to have a similar response to Blue-headed Vireo. However, they forage primarily on seeds (with some fruits; Middleton 1998), which might be more abundant in dry conditions (Wright *et al.* 1999). El Niño events are associated with relatively mild, dry winters in Alberta (Kiladis and Diaz 1989, New *et al.* 2001, Environment Canada 2003). Given that they appeared to be affected by the severity of winter weather at Meanook, I did not expect Black-capped Chickadees to be positively associated with the SOI. However, El Niño events are also associated with more spring storms in this region, which could negatively affect survival (Kiladis and Diaz 1989). Dry weather would also result in less snow on the ground, and reduce the availability of snow holes they use for roosting (C. St. Clair, personal communication).

Other Effects

Phenology was expected to influence abundance of migratory species by influencing where they chose to stop and breed. Although breeding-site fidelity in songbirds is thought to be high, neotropical migrants have a limited period in which to breed and may be forced to breed elsewhere if weather is inclement. As expected, no residents or short-distance migrants were correlated with phenology. Migrants that respond negatively to phenology may be stopping south of the study areas, while migrants that respond positively may be stopping at the study sites rather than breeding farther north. Species that responded positively to phenology tended to have the limits of their breeding distribution extend farther north than those that responded negatively to phenology (Van Horn and Donovan 1994, James 1998, Middleton 1998, Rimmer and McFarland 1998,

Cimprich *et al.* 2000, Wyatt and Francis 2002), weakly supporting this hypothesis. Stronger support for some species (Chipping Sparrow, Red-eyed Vireo, Rose-breasted Grosbeak and Tennessee Warbler) is provided by positive correlations between phenology and the indices of migration at two banding stations in Alberta, Beaverhill Bird Observatory (located south of the study sites) and Lesser Slave Lake Bird Observatory (located west-northwest of the study sites; Badzinski and Francis 2000).

Abundance of Least Flycatchers was lower in years following high red squirrel abundance for 10 years of data from Calling Lake, not surprising given other work identifying nest predation as being very important in this species (Briskie 1994). Least Flycatchers are characterized as infrequent hosts of Brown-headed Cowbirds (Briskie 1994), and were in fact positively associated with increased Cowbird abundance in the previous summer for most models. Ovenbirds, frequent hosts of Brown-headed Cowbirds (Van Horn and Donovan 1994), were negatively correlated with Cowbird abundance for 8 years of data from Calling Lake. Brown-headed Cowbird nest parasitism in other species, such as Ovenbirds, could benefit Least Flycatchers, presumably by reducing competition for food or other resources. Least Flycatcher has one of the most compressed breeding seasons known, requiring 58 days to raise young to independence but spending only 64 days on their breeding grounds (Briskie 1994). Furthermore, the energetic cost of feeding young is high, approximately 380% of the standard metabolic rate, compared to only 220% for Red-eyed Vireos (Holmes *et al.* 1979). Thus, any abandonment of parasitized nests by species that compete with Least Flycatcher for food could reduce the cost of raising young and increase fledging success in Least Flycatcher.

Conclusion

It is not clear whether Moran effects or dispersal might be more important in synchronizing the population dynamics of these species. Many species were correlated both with factors postulated to act through dispersal and with those postulated to work through Moran effects, suggesting that more than one mechanism is synchronizing population dynamics. Phenology may be a mechanism that desynchronizes population dynamics by reducing site fidelity and increasing mixing of populations; it was found to

be important for nearly half the species. Other mechanisms (e.g. intrinsic mechanisms such as territoriality) could also influence the dynamics of these species.

My results suggest that species respond independently to the factors examined here. Although I examined only 15 species, I could not identify any response guilds (*sensu* Szaro 1986). This has worrying implications for our ability to use one or a few indicator species to monitor the songbird community of boreal mixedwood forests, since we would expect that species that respond in similar ways to anthropogenic disturbance to also respond in similar ways to natural disturbances.

The relatively short timeseries used in this study may have prevented me from clearly identifying the factors that are important in driving the population dynamics of these species, and in synchronizing those dynamics over regional scales. In particular, the lack of consistency in results at the two study sites is somewhat worrying. Although differences in landscape context of the two sites may mean the sites are not true replicates, these results suggest that some of the relationships identified may be spurious. Extension of this study in time and space will be necessary to clearly identify the large-scale factors influencing the population dynamics of songbirds in the boreal mixedwood forests of North America.

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Table 4.1. Factors that were significantly correlated with changes in abundance of 15 forest songbirds in either linear regression model (the models using all bird data but excluding phenology, or the pre-2000 models including phenology). The type of correlation (positive + or negative -) is also noted. A significance level of p=0.10 was used since the analysis was exploratory in nature. Parameter estimates and exact p-values can be found in Appendix 4.

Species	Meanook[#]	Calling Lake	Effects[*]
Black-capped Chickadee	- winter weather, + breeding weather	+ SOI [§]	M
Blue-headed Vireo	+ fire, - SOI	- fire, - phenology, - breeding weather, + spruce budworm	D,M,P
Chipping Sparrow	+ SOI, + phenology	- fire	D,M,P
Connecticut Warbler	none	- breeding weather, - fire, + spruce budworm, + SOI	D,M
Least Flycatcher	none	none	none
Mourning Warbler	none	none	none
Ovenbird	- phenology, + fire	none	D,P
Pine Siskin	N/A	none [§]	none
Rose-breasted Grosbeak	+ fire, + phenology	none	D,P
Red-breasted Nuthatch	N/A	none [§]	none
Red-eyed Vireo	+ fire, + SOI, + phenology	+ spruce budworm, - fire	D,M,P
Tennessee Warbler	+ SOI, + phenology	+ phenology	M,P
Winter Wren	N/A	none	none
White-throated Sparrow	- fire	- breeding weather, - fire	D,M
Yellow-bellied Sapsucker	none	- breeding weather, - fire	D,M

[#] Models for Meanook did not include spruce budworm since an outbreak occurred within 100km of the site only in 1997.

[*] Dispersal-mediated effects (D), Moran effects (M) or phenology (P) were correlated with population dynamics at one or both sites.

[§] Models including all potential factors (cone crop, breeding weather, spruce budworm abundance, fire, SOI, phenology, and winter weather for residents) could not be fit due to limited sample size. Therefore, table includes only factors found significant in the 1993-2003 models that excluded phenology as a potential factor.

Table 4.2. Correlations between the number of red squirrels seen or heard during point counts with residuals from models fitting songbird abundance as a function of covariates at the Calling Lake and Meanook sites. Two sets of models were fit: the first used all bird data (1990-2002 at Meanook, 1993-2002 at Calling Lake) but excluded phenology, the other used only pre-2000 bird data but included phenology. Bold font indicates correlations that are significant at a multiple comparison error rate of 0.10 (i.e. an individual p-value ≤0.015; see *Covariates*); shaded cells indicate no model was fit.

	Calling Lake				Meanook			
	1993-1999		1993-2002		1990-1999		1990-2002	
	ρ	p-value	ρ	p-value	ρ	p-value	ρ	p-value
Black-capped Chickadee			0.13	0.73	-0.49	0.18	-0.21	0.52
Blue-headed Vireo	0.67	0.15	0.62	0.08	0.25	0.51	0.17	0.61
Chipping Sparrow	0.26	0.62	-0.41	0.27	0.05	0.90	-0.36	0.26
Connecticut Warbler	0.79	0.06	-0.08	0.82	0.76	0.02	0.32	0.31
Least Flycatcher	-0.86	0.03	**-0.90**	**0.001**	-0.58	0.10	-0.61	0.03
Mourning Warbler	-0.10	0.85	-0.42	0.26	-0.06	0.87	-0.08	0.81
Ovenbird	0.89	0.02	0.32	0.41	-0.29	0.45	-0.04	0.90
Pine Siskin			0.19	0.63				
Rose-breasted Grosbeak	0.64	0.17	-0.22	0.57	-0.31	0.41	-0.27	0.39
Red-breasted Nuthatch			-0.03	0.93				
Red-eyed Vireo	-0.79	0.06	-0.25	0.52	0.52	0.15	0.11	0.73
Tennessee Warbler	0.74	0.10	-0.10	0.80	-0.15	0.70	-0.39	0.21
Winter Wren	0.61	0.20	-0.01	0.98				
White-throated Sparrow	0.77	0.07	-0.42	0.27	-0.02	0.95	-0.08	0.81
Yellow-bellied Sapsucker	-0.77	0.07	0.07	0.86	-0.09	0.82	-0.13	0.68

Table 4.3. Correlations between the number of Brown-headed Cowbirds seen or heard during point counts with residuals from models fitting songbird abundance as a function of covariates at the Calling Lake and Meanook sites. Two sets of models were fit: the first used all bird data (1990-2002 at Meanook, 1993-2002 at Calling Lake) but excluded phenology, the other used only pre-2000 bird data but included phenology. Bold font indicates correlations that are significant at a multiple comparison error rate of 0.10 (i.e. an individual p-value ≤0.015; see *Covariates*); shaded cells indicate no model was fit.

	Calling Lake				Meanook			
	1993-1999		1993-2002		1990-1999		1990-2002	
	ρ	p-value	ρ	p-value	ρ	p-value	ρ	p-value
Black-capped Chickadee			-0.36	0.34	0.62	0.07	0.43	0.17
Blue-headed Vireo	-0.55	0.26	-0.52	0.15	-0.14	0.71	-0.16	0.63
Chipping Sparrow	-0.29	0.58	-0.03	0.94	-0.08	0.83	-0.01	0.96
Connecticut Warbler	-0.87	0.02	-0.02	0.95	-0.45	0.23	-0.20	0.54
Least Flycatcher	0.77	0.07	**0.83**	**0.01**	**0.80**	**0.01**	**0.74**	**0.01**
Mourning Warbler	0.24	0.65	0.31	0.41	-0.33	0.38	-0.24	0.45
Ovenbird	**-0.93**	**0.01**	-0.46	0.22	0.08	0.84	0.08	0.81
Pine Siskin			-0.51	0.16				
Rose-breasted Grosbeak	-0.70	0.13	-0.11	0.78	0.58	0.10	0.32	0.31
Red-breasted Nuthatch			-0.28	0.46				
Red-eyed Vireo	0.72	0.11	0.48	0.19	0.15	0.71	0.04	0.91
Tennessee Warbler	-0.76	0.08	-0.25	0.51	-0.13	0.73	-0.04	0.91
Winter Wren	-0.77	0.07	-0.37	0.33				
White-throated Sparrow	-0.68	0.14	0.43	0.25	-0.21	0.58	-0.13	0.69
Yellow-bellied Sapsucker	0.68	0.14	0.24	0.54	0.10	0.80	0.13	0.69

Figure 4.1. Location of the Calling Lake and Meanook study sites within Alberta.

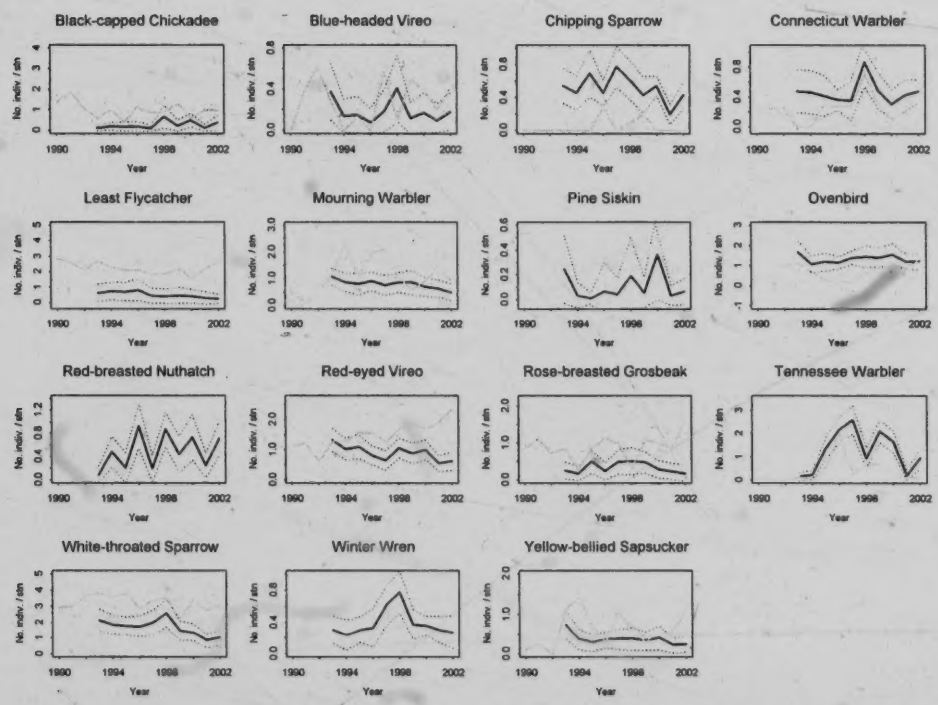

Figure 4.2. Population dynamics of 15 boreal songbirds at Calling Lake (black) and Meanook (grey). Dotted lines are approximate 95% confidence intervals (2xSE) for variability between clusters.

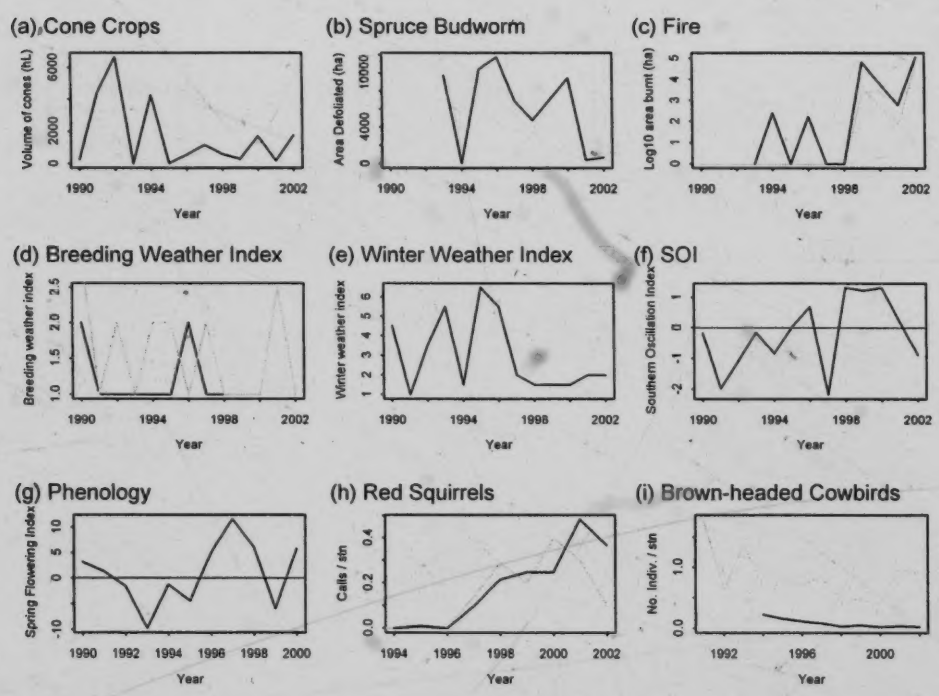

Figure 4.3. Timeseries of covariates, with lags as entered in models. Plots are: (a) volume of white spruce cones collected in previous fall; (b) area defoliated by spruce budworm in surrounding region during previous summer in region surrounding Calling Lake; (c) $\log_{10}$ of area burnt by forest fires (+ 1ha) during previous summer in region surrounding Calling Lake (black) and Meanook (grey); (d) index of severe weather during previous breeding season of residents (black) and migrants (grey); (e) index of severe weather during wintering season of residents; (f) southern oscillation index, averaged over previous winter; (g) spring flowering index; (h) number of red squirrel calls observed during point counts at Calling Lake (black) and Meanook (grey); (i) number of Brown-headed Cowbirds observed during point counts at Calling Lake (black) and Meanook (grey).

Chapter 5: Implications for designing studies of songbird population dynamics.

Introduction

Songbirds are commonly used as indicators of ecosystem integrity (e.g. Croonquist and Brooks 1991, O'Connell *et al.* 2000). Therefore, we need to understand their population dynamics under natural conditions in order to provide a baseline for comparison with dynamics in potentially disrupted areas. Here, I provide information that may help in the design of monitoring programs, based on earlier studies of population dynamics of songbird communities in the boreal mixedwood forest of Alberta (Chapters 2 through 4).

Carlson and Schmiegelow (2002) also used control data from the Calling Lake site as the basis for a simulation study examining the cost and efficiency of different point-count sampling designs. They examined temporal variability and the number of replicates used, and conducted a detailed cost-benefits analysis. My thesis complements this work by examining two more aspects of sampling: potential biases in detectability using point counts and estimating appropriate spatial scales for sampling.

Songbirds are monitored using a variety of techniques, which vary in the effort and cost required and the quality of data obtained. Detailed surveys of demography, using techniques such as mist netting or nest searching, provide high quality data but are expensive and limit the area that may be surveyed (Ralph *et al.* 1983). Faster techniques, such as point or transect counts, greatly increase the area that can be surveyed but provide information only on relative densities (Ralph *et al.* 1983).

Here, I limit discussion to the design of studies using point counts as the survey technique, although some of the considerations may also be applicable to other techniques. I assume the objective of the study is to quantify changes in density for some purpose, such as identifying population declines. When designing such a survey, researchers are faced with many questions: How many point count stations should comprise a sampling unit? How widely should I space my sampling units? How many

sampling units will I need to detect a given population decline? Here, I attempt to outline how a researcher might approach these problems.

Detectability

In songbird surveys, detectability is defined as the proportion of individuals present at a location that are detected. In most circumstances, the actual proportion of individuals detected is unimportant as long as detectability is constant; in other words, an index of abundance is usually suitable as long as it is linearly related to true density.

Unfortunately, many factors can influence detectability during surveys. Most researchers design their surveys to minimize common environmental variables and observer differences known to influence detectability, for example by limiting surveys to dry, calm days and by rotating observers. However, density itself can sometimes influence detectability; territorial behaviours such as singing can increase at high population densities (Mönkkönen and Aspi 1997). A "good" index will measure a constant proportion of the true abundance over all population densities (Link and Nichols 1994, Johnson 1995, Pollock *et al.* 2002, Rosenstock *et al.* 2002, Thompson 2002).

In Chapter 2, I compared estimates of abundance from an intensive survey method, spot-mapping (a territory mapping method), with estimates of abundance from point count surveys to determine whether point counts were a good index of abundance, as defined above. As in other studies (e.g. Emlen 1971, Franzreb 1976, Svensson 1981, Szaro and Jakle 1982, Cyr *et al.* 1995), point counts were correlated with spot mapping estimates at the scale of a spot mapping grid (typically 10-20ha in forest; Bibby *et al.* 1992). However, this result was not consistent at smaller spatial scales. At the scale of a single point count station (3.1 ha), I found that point counts were poorly correlated with spot mapping estimates, except for Least Flycatcher (*Empidonax minimus*; Chapter 2). However, point counts appeared to be linearly related to the number of territorial individuals; although sampling errors were large, detectability did not appear to depend on density (Chapter 2). The relationships were stronger for species with smaller territories. Previous studies have found significant linear correlations for some species

(e.g. DeSante 1981, DeSante 1986, Tarvin *et al.* 1998, Jones *et al.* 2000), but not for others (e.g. DeSante 1981, DeSante 1986). Point count stations also survey non-territorial individuals ("floaters") and individuals moving outside their territorial boundaries (Granholm 1983, Verner 1985), which might increase sampling errors and reduce the efficiency of this sampling technique.

Although point counts are a rapid survey technique, the large amount of sampling error associated with this technique suggest its use be carefully examined when designing monitoring programs. Point counts allow more sites to be surveyed than with labour-intensive techniques like spot mapping, but the associated sampling errors could potentially impact statistical tests more than the increase in sample size (Gibbs *et al.* 1998).

There is another reason why simple point counts may not be the best technique to use in a monitoring program: density may not always reflect habitat quality due to source/sink dynamics (Brawn and Robinson 1996), territoriality (Fretwell and Lucas 1969) and the lagged effects of temporal variability (Van Horne 1983). Therefore, monitoring programs which survey only for density could give misleading estimates of population trends. Incorporating techniques that survey reproductive success into monitoring programs may provide better estimates of population dynamics, and possibly increase our ability to foretell population declines (Ralph *et al.* 1993). This could be accomplished by sub-sampling some sites within the monitored area using intensive surveys of reproductive success (e.g. nest searching and monitoring). However, recording indicators of reproductive activity during point counts, either passively (Vickery *et al.* 1992) or using mobbing calls (Gunn *et al.* 2000), can also provide an index of reproductive success with much less cost, particularly for the more abundant species (Rangen *et al.* 2000).

Spatial Scale

We know that the spatial scale of a study influences the observed dynamics of a population (Allen and Starr 1982, Carlile *et al.* 1989, Turner *et al.* 2001), but determining

an appropriate spatial scale for studies is difficult. Many researchers indirectly approach this problem by attempting to find the scale where covariates, such as habitat elements, are most highly correlated with population dynamics (e.g. Huhta *et al.* 1998). Although this approach may be useful in determining the scale at which covariates influence population dynamics, it does not help to identify an appropriate spatial scale at which to measure the population dynamics themselves.

In Chapter 3, I suggested that appropriate spatial scales for studies of population dynamics are given by the range of scales where a single pattern of population dynamics occurs. The lower end of this range may be the optimal size of sampling units (Greig-Smith 1952, Kershaw 1957, Mead 1974, Carlile *et al.* 1989), while the upper end of this range defines a region within which sampling units are not independent of each other (Carlile *et al.* 1989, Lichstein *et al.* 2002). This is a multi-year approach, unlike most studies of spatial scale in songbirds (e.g. Brown *et al.* 1995, Beard *et al.* 1999, Moskát 2000, Lichstein *et al.* 2002, but see Koenig 1998, 2001). Single-year methods probably give more variable estimates of spatial scale than multi-year methods, since environmental variables might influence the scale observed in any single year.

I found that the optimal size of sampling units differed between species, ranging from one to six 3.1 ha point-count stations (Chapter 3). However, sampling units greater than six stations in size were not examined, so optimal sizes could be larger than estimated. The region where sampling units were correlated (i.e. not independent) were ≥ 8km for 15 of the 25 species examined at one 10×10km site, Calling Lake, in northern Alberta (Chapter 3). However, population dynamics for 12 of these species are available at another site, Meanook, 70km south of Calling Lake. I extracted timeseries at the two study sites as in Chapter 4, and examined whether the correlation between the two sites was consistent with spatial autocorrelation to ≥ 70km. Six of these species (Least Flycatcher, Mourning Warbler *Oporornis philadelphia*, Ovenbird *Seiurus aurocapillus*, Tennessee Warbler *Vermivora peregrina*, White-throated Sparrow *Zonotrichia albicollis* and Yellow-bellied Sapsucker *Sphyrapicus varius*) had correlations in population dynamics between sites that were consistent with those within the Calling Lake site. It is not clear whether this autocorrelation would be significant for most species, but the

population dynamics of Tennessee Warblers are likely to be significant beyond 70km, given the tight confidence intervals observed within the Calling Lake site (Chapter 3).

Multi-year approaches, like those of Chapter 3 and Koenig (1998, 2001) seem more likely to provide a reliable estimate of appropriate spatial scales than single-year studies. However, when designing a monitoring program in a new area or for new species, we don't want to spend several years estimating appropriate spatial scales. Therefore, is there any way to predict an appropriate scale *a priori*? Neither body mass nor territory size were significantly correlated with the scales of spatial autocorrelation (Chapter 3, Koenig 1998). Population dynamics can become synchronized in space through Moran effects (stochastic events that perturb reproductive success or survival over a large area) or dispersal (Ranta *et al.* 1995, Ranta *et al.* 1999). If we know the environmental or habitat variables that synchronize population dynamics, we could use the spatial scale of these variables as an estimate of the appropriate scales for monitoring birds. However, most species appear to respond to a number of potentially synchronizing factors, and species appeared to respond independently (Chapter 4). Therefore, the simplest approach may be to try and directly estimate appropriate spatial scales using previously collected data. For example, Breeding Bird Survey data could be used to estimate maximum extents of synchrony in population dynamics, even though they are not amenable to estimating minimum extents of synchrony.

Temporal Variability

Large amounts of variability reduce the ability to detect significant trends in population dynamics, so monitoring programs should be designed to minimize obvious sources of sampling error. However, true density can also vary over time, so we must carefully design monitoring programs so the statistical power is sufficient to detect important trends despite this variation (Fairweather 1991, Gibbs *et al.* 1998, Carlson and Schmiegelow 2002). Therefore, we need estimates of the temporal variability we can expect under control conditions. Although the variability in population dynamics observed in the past may not be indicative of the variability we can expect in the future

(Underwood 1991), they do provide a rough approximation that can be used to estimate the number of samples necessary for a given study.

We can estimate this variability for species in the mixedwood boreal forest of northern Alberta using timeseries from the Calling Lake and Meanook study sites (Chapter 4). Temporal variability in timeseries is usually quantified using the coefficient of variation. However, the usual estimator of the coefficient of variation is biased when sample sizes are small (Sokal and Braumann 1980). Therefore, as well as the usual estimate, I used a modified coefficient of variation that approximately corrects for this bias (Sokal and Braumann 1980):

$$CV^* = \left(1 + \frac{1}{4n}\right)\frac{s}{\bar{y}}$$

$$se(CV^*) = \left[\frac{CV^{*2}}{2n}\left(\frac{n}{n-1} + 2CV^{*2}\right)\left(1 + \frac{1}{4n}\right)^2\right]^{0.5}$$

Although there were differences in the modified coefficients of variation between the Calling Lake and Meanook sites, the differences were not significant except for Ovenbird (Table 5.1). Carlson and Schmiegelow (2002) estimated much larger coefficients of variation for Black-capped Chickadee (*Poecile atricapillus*), and comparable estimates for White-throated Sparrow using the first 6 years of data at Calling Lake, although it is difficult to directly compare estimates due to differences in length of time series and spatial scales of data used. At a more comparable spatial scale, coefficients of variation for eight of these species are also available calculated by Holmes *et al.* (1986), for 16 years of data in New Hampshire (the site covers approximately half the area of Calling Lake). Coefficients of variation for Red-eyed Vireo (*Vireo olivaceus*), Rose-breasted Grosbeak (*Pheucticus ludovicianus*) and Yellow-bellied Sapsucker are consistent between the two studies (i.e. estimated coefficient of variation in New Hampshire falls within an approximate 95% confidence interval for the Alberta sites), but were higher in the New Hampshire study for the remaining species (Black-capped Chickadee, Blue-headed Vireo *Vireo solitarius*, Least Flycatcher, Ovenbird and Winter Wren *Troglodytes troglodytes*). Since coefficients of variation tend to increase with the length of timeseries (Pimm and Redfearn 1988, McArdle *et al.* 1990) and no estimate of precision was provided by Holmes *et al.* (1986), it is difficult to determine whether population dynamics of the latter species are really more variable at the New Hampshire site.

Within sites, some significant differences were observed between species. At Calling Lake, the most variable species were the three residents (Black-capped Chickadee, Pine Siskin *Carduelis pinus* and Red-breasted Nuthatch *Sitta canadensis*) and the Tennessee Warbler. No such pattern was observed at Meanook, although Tennessee Warbler was still highly variable. Helle and Mönkkönen (1986), in a Finnish study, found that residents and short-distance migrants were more variable than long-distance migrants, but a similar pattern was not observed in New Hampshire (Holmes *et al.* 1986). Thus, it is not clear if migratory guilds differ in temporal variability.

Recommendations

Individual point count stations generally seem to be a constant proportion of the number of territorial individuals, but this assumption should be validated. Point counts also have large sampling errors for many species, particularly for those with larger territories. Future studies should consider modifications to a 100m-radius, 5-minute point-count that might reduce sampling variation. For example, the use of mobbing calls may improve detectability, as well as providing an estimate of reproductive success (Gunn *et al.* 2000). However, it is not yet clear whether this technique also reduces the sampling error associated with fixed-radius point counts.

Chapter 3 provides a technique to estimate the number of point count stations that comprise an optimal sampling unit. The use of optimal unit sizes will minimize sampling variation at that level, improving all estimates subsequently derived from that data. Designs should include replication at all levels of the sampling design, so that sampling variation can be quantified and separated from underlying temporal variation (Link and Nichols 1994). Carlson and Schmiegelow (2002) looked at how many replicate point-count stations within a site were optimal, but did not directly examine optimal sampling unit sizes. In Chapter 3, I decoupled the effect of increasing the number of replicates from the determination of appropriate spatial scale by using a randomization test to determine optimal unit size.

The maximum scale of synchrony in population dynamics (Chapter 3) can be used to identify regions where sampling units will not be independent. Multi-year approaches to

estimation of the maximum scale of synchrony in population dynamics are recommended (e.g. Chapter 3, Koenig 1998, 2001). Since it is difficult to identify which factors are synchronizing population dynamics over large spatial scales (Chapter 4), I recommend empirical estimates based on previously collected population density data.

Chapter 4 suggested that species respond independently to natural disturbances. Thus, I suggest it may be difficult to find indicator species that are suitable for monitoring the songbird community in boreal mixedwood forests. Monitoring programs should not rely on the indicator species concept unless emprical evidence suggests that response guilds (Szaro 1986) can be documented.

Power analyses should be conducted when designing any monitoring program, to ensure that the design is sufficient to detect the expected changes in population density (Fairweather 1991, Carlson and Schmiegelow 2002). Such an analysis is outside the scope of this paper; however, I have provided estimates of temporal variability (exclusive of sampling variation) that could be used to estimate power for a proposed design.

Priorities for future research fall in three areas. Improved empirical estimates of optimal sampling units should be undertaken; Chapter 3 was limited by the extent and layout of the sampling grid of control plots. A network of sampling units with a larger spatial extent should be undertaken so maximum scales of synchrony in population dynamics can be estimated. Finally, more research into the factors that promote spatial synchrony in population dynamics of songbirds might allow us to predict appropriate spatial scales in new areas *a priori*.

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Table 5.1. Standard (CV) and modified (CV*) coefficients of variation for fifteen boreal songbird species at two study sites in northern Alberta. Approximate confidence intervals can be constructed as estimate ± 1.96×SE. Italics indicate timeseries where normality is violated, suggesting estimates may not be reliable (Sokal and Braumann 1980).

	Calling Lake			Meanook		
	CV	CV*	SE(CV*)	CV	CV*	SE(CV*)
Black-capped Chickadee	*0.72*	*0.73*	*0.25*	*0.37*	*0.38*	*0.09*
Chipping Sparrow[1]	0.31	0.32	0.08	*2.08*	*2.12*	*1.34*
Connecticut Warbler[1]	0.33	0.34	0.09	0.83	0.84	0.27
Least Flycatcher	0.37	0.38	0.10	0.17	0.17	0.04
Mourning Warbler	0.20	0.20	0.05	0.58	0.59	0.16
Ovenbird	0.15	0.15	0.04	0.52	0.53	0.14
Pine Siskin	*1.05*	*1.08*	*0.46*	–	–	–
Red-breasted Nuthatch	0.62	0.64	0.20	–	–	–
Rose-breasted Grosbeak	*0.42*	*0.43*	*0.12*	*0.38*	*0.39*	*0.09*
Red-eyed Vireo	0.27	0.28	0.07	0.29	0.30	0.07
Solitary Vireo	*0.59*	*0.61*	*0.19*	0.80	0.81	0.25
Tennessee Warbler	0.72	0.74	0.25	1.45	1.48	0.69
White-throated Sparrow	0.31	0.32	0.08	0.14	0.15	0.03
Winter Wren	*0.44*	*0.45*	*0.13*	–	–	–
Yellow-bellied Sapsucker	0.39	0.40	0.11	0.73	0.74	0.22

[1] Scientific names are *Spizella passerina* (Chipping Sparrow) and *Oporornis agilis* (Connecticut Warbler).

Appendix 1: Additional results for Chapter 2.

Table A1.1. Test of correlations between two transformations of maximum and mean point count abundance for 12 species at Calling Lake (Chapter 2): simple non-jackknifed log transformations and jackknifed estimators of log transformations. Although the simple transformations can result in biased estimates, the strong correlations suggest bias is minimal in this case.

	Correlation	p-value
Maximum point-count abundance	0.907	0.000
Mean point-count abundance	0.914	0.000

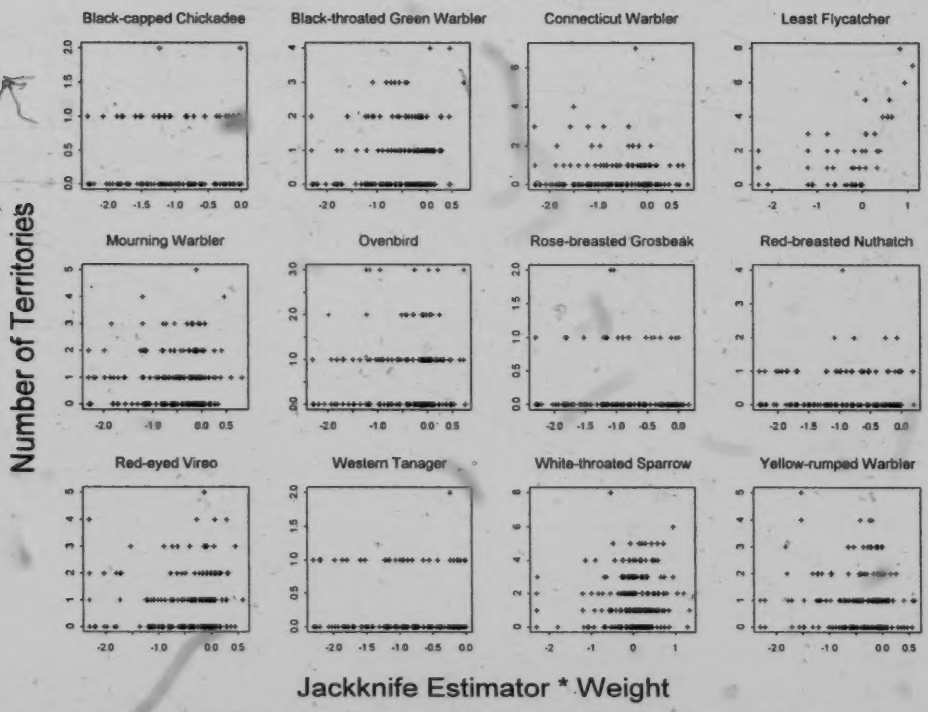

Figure A1.1. Relationship between the number of territories from spot mapping and the jackknife estimator of maximum point-count abundance, multiplied by sampling weights (proportion of point-count station overlapping spot-mapping grid). This is the relationship modelled. Species names are given in Chapter 2.

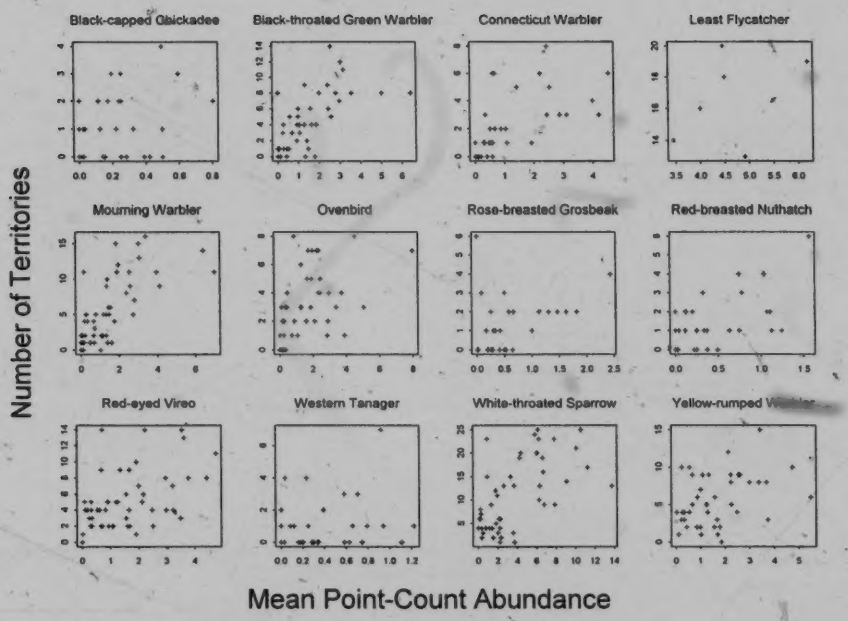

Figure A1.2. Relationship between number of territories in a spot-mapping grid and the maximum point-count abundance summed over all stations within that grid. Species names are given in Chapter 2.

Appendix 2: Comparison of point-count abundance and number of territories identified by spot-mapping, irrespective of territory overlap.

Introduction

In Chapter 2, I looked at whether detectability in point counts depended on population density by comparing density estimates from point-counts and spot-mapping. In order to make this comparison at the point-count station scale, the number of territorial individuals associated with a station needed to be defined. I chose to define the number of territorial individuals as the number of individuals with at least 50% of their estimated territory within the point count station (Chapter 2). However, model fits were often poor (Chapter 2) suggesting this definition might not be optimal. Here, I summarize results from analyses using an alternate definition: the number of territorial individuals is the number of individuals with any fraction of their estimated territory within the point count station.

As in Chapter 2, I checked whether index counts could be compared in time or space without correction by determining if a linear model was appropriate. I also tested if territory size influenced the efficiency of point counts and compared models with mean and maximum point count abundance to determine which was more closely related to spot mapping abundance.

Methods

The same data was used as in Chapter 2, except that true abundance was estimated as the number of individuals with any fraction of their spot-mapped territory intersecting an individual point count plot. All statistical analyses follow Chapter 2. Common and scientific names of species examined are listed in Table A2.1.

Results

Most species show moderately linear relationships between the number of territories and the jackknife estimators at the scale of a point count station (Figures A2.1 and A2.2). Nevertheless, the relationship was weaker than the grid-scale estimates (Chapter 2, Appendix 1). Models including space through a random effect of grid were better in all cases except for maximum point-counts of Least Flycatcher (Table A2.2). Residual plots show no evidence of non-linearity (Toms, unpublished results).

Maximum and mean point count abundance generally had similar results overall. However, maximum point count generally produced better model fits (as measured by r_c; Table A2.2) and had slopes that were closer to one (Table A2.3). There was no significant correlation between territory size and model fit (as measured by r_c; rho=-0.41, p=0.17 for maximum point count; rho=-0.46, p=0.12 for mean point count), as predicted.

Discussion

As found with an alternate definition of the number of territorial individuals associated with a point-count station (Chapter 2), I found that both maximum and mean point-counts were linearly related to the number of territorial individuals. Furthermore, maximum point counts were again a more sensitive index of abundance and had slightly better model fits. Maximum point counts appear to be a better index for the species examined here, no matter the definition of territorial individuals used. Consistent with Chapter 2, models including a random effect of spot-mapping grid fit much better than the other models (fixed effects only, random effect of year).

The relationship between point-count and spot-mapping abundance was much stronger with this definition of territorial individuals, as evidenced in the plots and model fits. This seems to indicate that individuals with small portions of territories falling within a point-count station are being observed in the point counts. This could result from poor distance estimation, if observers in the point counts consistently overestimated the 100m station radius (i.e. consistently observed all individuals within a larger radius).

Alternatively, this could result from songbird behaviour; males tend to sing more at the edges of their territories than in the centers (e.g. Hudon 1999, Cimprich *et al.* 2000). Because most registrations in point counts are of singing males (Gibbs and Wenny 1993, Rosenstock *et al.* 2002), point-count abundance may be proportional to the total length of territorial boundaries in the plot rather than the total fraction of territories within the plot. Interestingly, model fit was not significantly correlated with territory size, as it was in Chapter 2. In Chapter 2, species with small territories were more likely to have a majority of their territory within the spot-mapping plot, resulting in a higher degree of similarity in the two estimates of territorial individuals.

In conclusion, results using this alternate definition of the number of territorial individuals within a point-count station are consistent with Chapter 2. However, this definition resulted in better model fits. I propose two hypotheses to explain this result: (1) point count observers consistently overestimated the radius of the plot, and (2) point counting is more representative of territorial boundaries than of the territories themselves. Further work will be required to determine why these differences occur.

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Table A2.1. List of common and scientific names of species examined.

Common Name	Scientific Name
Black-capped Chickadee	*Poecile atricapillus*
Black-throated Green Warbler	*Dendroica virens*
Connecticut Warbler	*Oporornis agilis*
Least Flycatcher	*Empidonax minimus*
Mourning Warbler	*Oporornis philadelphia*
Ovenbird	*Seiurus aurocapillus*
Red-breasted Nuthatch	*Sitta canadensis*
Red-eyed Vireo	*Vireo olivaceus*
Rose-breasted Grosbeak	*Pheucticus ludovicianus*
Western Tanager	*Piranga ludoviciana*
White-throated Sparrow	*Zonotrichia albicollis*
Yellow-rumped Warbler	*Dendroica coronata*

Table A2.2. Akaike weights and r_c values for the three generalized linear models fitting spot-mapping abundance as a function of point-count abundance: a model with only fixed effects, a model including a random effect of spot-mapping grid, and a model including a random effect of year. Akaike weights represent the probability that a given model is the best in the set tested; r_c values are a measure of model fit, where a perfect fit corresponds to $r_c = 1$, and a significant lack of fit corresponds to $r_c \leq 0$. The best-fitting model in the set is in bold type.

Species	Point Count Data Type	No Random		Grid Random		Year Random	
		Akaike weight	r_c	Akaike weight	r_c	Akaike weight	r_c
Black-capped Chickadee	Maximum	0.09	0.01	**0.78**	**0.18**	0.14	0.07
	Mean	0.09	0.00	**0.77**	**0.17**	0.14	0.07
Black-throated Green Warbler	Maximum	0.00	0.35	**1.00**	**0.62**	0.00	0.43
	Mean	0.00	0.23	**1.00**	**0.60**	0.00	0.33
Connecticut Warbler	Maximum	0.00	0.43	**1.00**	**0.65**	0.00	0.46
	Mean	0.00	0.41	**1.00**	**0.65**	0.00	0.43
Least Flycatcher	Maximum	**0.52**	**0.80**	0.29	0.80	0.19	0.80
	Mean	0.10	0.65	**0.86**	**0.69**	0.04	0.65
Mourning Warbler	Maximum	0.00	0.08	**1.00**	**0.41**	0.00	0.14
	Mean	0.00	0.02	**1.00**	**0.40**	0.00	0.09
Ovenbird	Maximum	0.00	0.32	**1.00**	**0.58**	0.00	0.38
	Mean	0.00	0.36	**1.00**	**0.59**	0.00	0.42
Red-breasted Nuthatch	Maximum	0.00	0.13	**0.89**	**0.47**	0.11	0.31
	Mean	0.00	0.08	**0.69**	**0.44**	0.31	0.30
Red-eyed Vireo	Maximum	0.00	0.15	**1.00**	**0.44**	0.00	0.15
	Mean	0.00	0.14	**1.00**	**0.43**	0.00	0.14
Rose-breasted Grosbeak	Maximum	0.00	0.08	**1.00**	**0.57**	0.00	0.31
	Mean	0.00	0.04	**1.00**	**0.57**	0.00	0.29
Western Tanager	Maximum	0.00	0.00	**1.00**	**0.65**	0.00	0.14
	Mean	0.00	0.00	**1.00**	**0.65**	0.00	0.14
White-throated Sparrow	Maximum	0.00	0.21	**1.00**	**0.60**	0.00	0.30
	Mean	0.00	0.16	**1.00**	**0.59**	0.00	0.28
Yellow-rumped Warbler	Maximum	0.00	0.02	**0.93**	**0.46**	0.07	0.28
	Mean	0.00	0.01	**0.94**	**0.46**	0.06	0.28

Table A2.3. Parameter estimates for best-fitting model of spot-mapping abundance as a function of point-count abundance. The set of models tested were: a model with only fixed effects, a model including a random effect of spot-mapping grid, and a model including a random effect of year.

	Point	Best	α		β		random effect	
Species	Count Data	Model	est.	SE	est.	SE	est.	SE
Black-capped	Maximum	grid	-0.87	0.23	0.15	0.14	0.51	0.20
Chickadee	Mean	grid	-0.90	0.25	0.12	0.16	0.51	0.20
Black-throated	Maximum	grid	0.05	0.23	0.42	0.08	0.85	0.22
Green Warbler	Mean	grid	0.09	0.26	0.38	0.09	0.94	0.23
Connecticut	Maximum	grid	-0.39	0.26	0.64	0.15	0.80	0.24
Warbler	Mean	grid	-0.31	0.29	0.62	0.17	0.88	0.25
Least	Maximum	fixed only	0.63	0.09	1.24	0.12	-	-
Flycatcher	Mean	grid	1.09	0.17	1.09	0.13	0.26	0.14
Mourning	Maximum	grid	0.53	0.14	0.15	0.06	0.52	0.12
Warbler	Mean	grid	0.53	0.15	0.08	0.07	0.55	0.13
Ovenbird	Maximum	grid	0.29	0.16	0.42	0.12	0.57	0.15
	Mean	grid	0.41	0.15	0.51	0.13	0.55	0.14
Rose-breasted	Maximum	grid	-0.92	0.35	0.17	0.12	1.09	0.31
Grosbeak	Mean	grid	-0.90	0.36	0.17	0.13	1.12	0.31
Red-breasted	Maximum	grid	-0.29	0.21	0.51	0.12	0.65	0.17
Nuthatch	Mean	grid	-0.23	0.23	0.50	0.14	0.67	0.18
Red-eyed Vireo	Maximum	grid	0.62	0.10	0.29	0.08	0.34	0.08
	Mean	grid	0.70	0.10	0.30	0.08	0.34	0.08
Western	Maximum	grid	-1.38	0.35	-0.03	0.14	0.13	0.28
Tanager	Mean	grid	-1.43	0.37	-0.07	0.17	1.13	0.28
White-throated	Maximum	grid	1.10	0.12	0.30	0.07	0.46	0.09
Sparrow	Mean	grid	1.18	0.11	0.27	0.08	0.46	0.09
Yellow-rumped	Maximum	grid	0.74	0.11	0.13	0.08	0.41	0.09
Warbler	Mean	grid	0.78	0.11	0.13	0.09	0.41	0.09

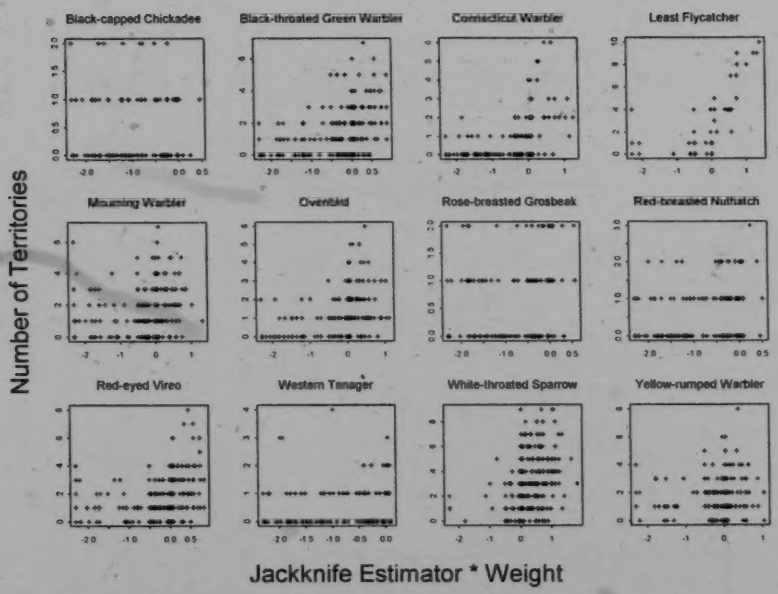

Figure A2.1. Relationship between the number of territories from spot mapping and the jackknife estimator of maximum point-count abundance, multiplied by sampling weights (proportion of point-count station overlapping spot-mapping grid).

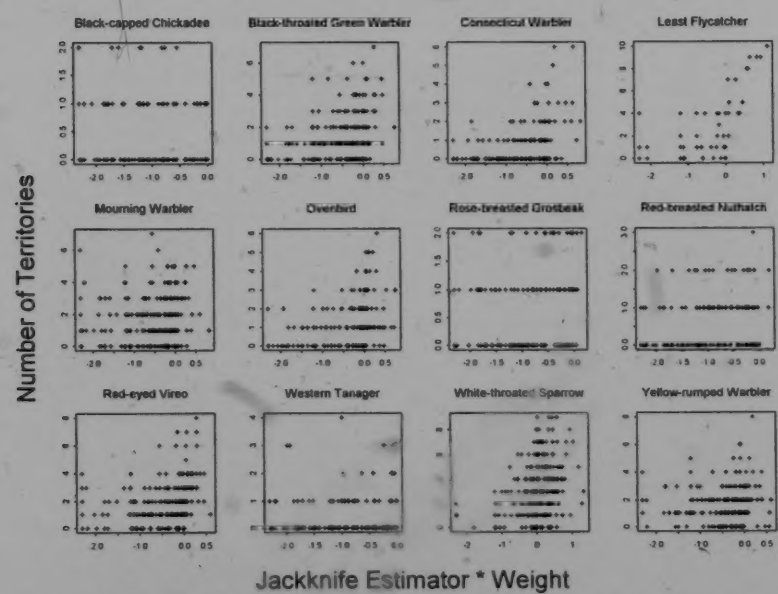

Figure A2.2. Relationship between the number of territories from spot mapping and the jackknife estimator of mean point-count abundance, multiplied by sampling weights (proportion of point-count station overlapping spot-mapping grid).

Appendix 3: Estimation of spatial scales of synchrony in population dynamics of songbirds at Meanook.

Introduction

In Chapter 3, I determined the spatial scales where population dynamics of 25 species at Calling Lake were synchronous. However, in order to compare population dynamics between Calling Lake and Meanook (Chapter 4), similar estimates were required at the Meanook study site. This appendix documents the estimation procedure and results at Meanook.

Methods

The Meanook site is located approximately 70 km south of Calling Lake (54°37' N, 113°20' W). Forest was similar in age and species composition to Calling Lake, but the site was located within an agricultural landscape. Seven point count stations were surveyed annually from 1990-2002 in a 140ha block of forest (Hannon 1993 and unpublished data). An additional four stations were surveyed for three or four consecutive years within this period.

At Meanook, point count surveys used unlimited distance plots, so I removed all observations in the "very far" distance class (roughly, distances greater than or equal to 200m). Points were surveyed for six min over four rounds at roughly two-three week intervals from the second week of May through the end of June. Annual abundance at each point was estimated as the maximum number of individuals observed over the four survey periods. Species surveyed are listed in Table A3.1.

Point count stations at Meanook were too dispersed to apply the minimum scale analysis of Chapter 3, so maximum spatial scales were determined by plotting the correlations of temporal abundance patterns from all pairs of point count stations as a function of distance between the stations. Otherwise, analyses follow Chapter 3.

Results and Discussion

Confidence intervals at Meanook were wide (Figure A3.1), so estimated patterns of spatial autocorrelation should be treated with caution. Black-capped Chickadee, Blue-headed Vireo, Least Flycatcher, Mourning Warbler and Yellow-bellied Sapsucker had similar levels of spatial autocorrelation, allowing for minor differences in trend. Yellow Warbler had generally lower spatial autocorrelation at Meanook, consistent with the lower confidence interval at Calling Lake. Ovenbird appeared to be autocorrelated over shorter distances than at Calling Lake. Nevertheless, most 90% confidence intervals overlapped, suggesting patterns of spatial autocorrelation are roughly comparable across the two sites. Thus, spatial scales deemed appropriate for Calling Lake data (Chapter 3) should be adequate for Meanook data and are preferable because they are more precise.

References

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Table A3.1. List of common and scientific names used.

Common Name	Scientific Name
Baltimore Oriole	*Icterus galbula*
Black-capped Chickadee	*Poecile atricapillus*
Blue-throated Vireo	*Vireo solitarius*
Hermit Thrush	*Catharus guttatus*
Least Flycatcher	*Empidonax minimus*
Mourning Warbler	*Oporornis philadelphia*
Ovenbird	*Seiurus aurocapillus*
Red-eyed Vireo	*Vireo olivaceus*
Rose-breasted Grosbeak	*Pheucticus ludovicianus*
Song Sparrow	*Melospiza melodia*
White-throated Sparrow	*Zonotrichia albicollis*
Yellow-bellied Sapsucker	*Sphyrapicus varius*
Yellow Warbler	*Dendroica petechia*

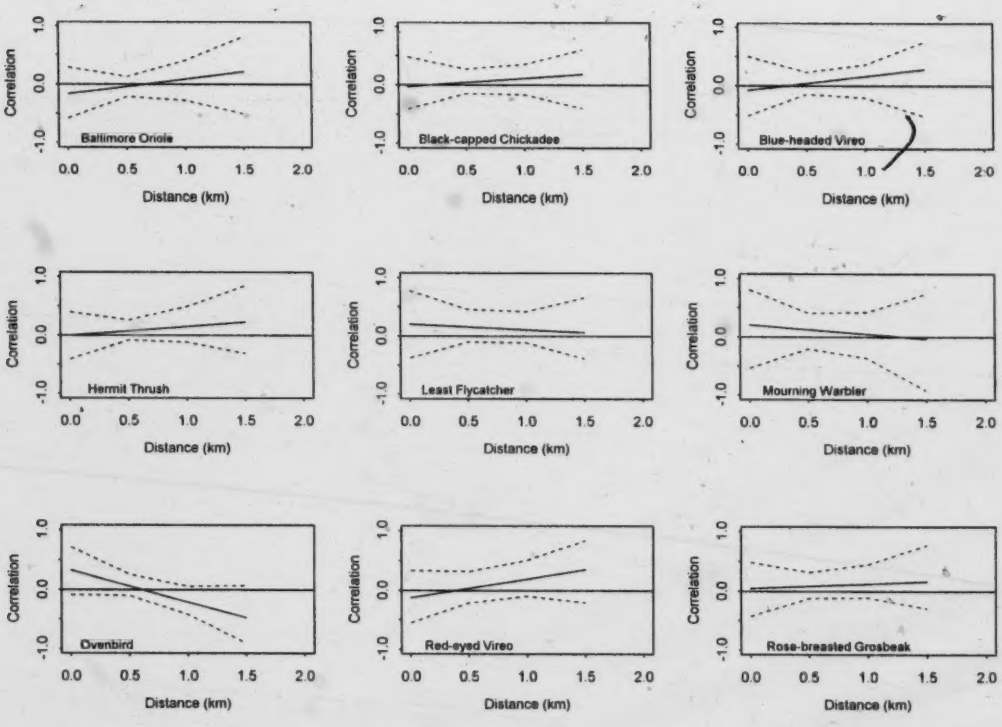

Figure A3.1. Spatial autocorrelation of temporal patterns at Meanook. Solid lines are estimates, dotted lines are 90% confidence intervals.

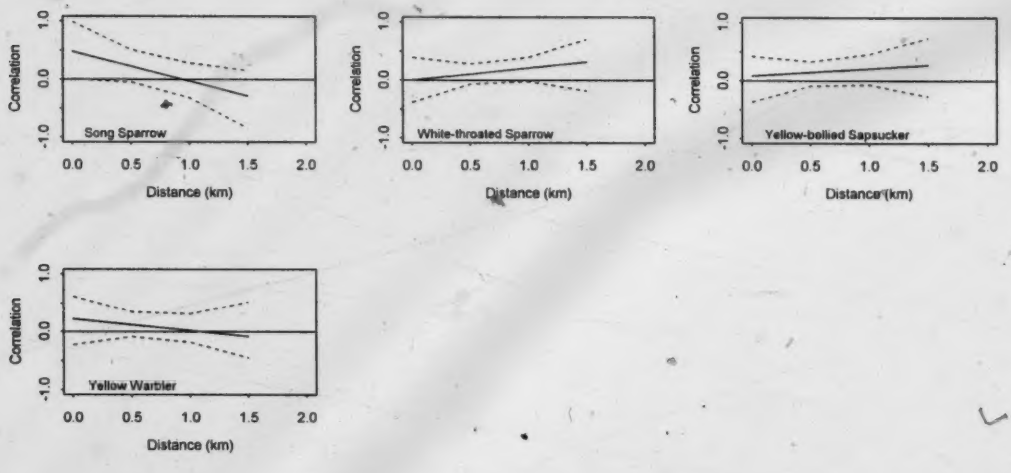

Figure A3.1 cont…

Appendix 4: Results from linear regression models of songbird population dynamics at Meanook and Calling Lake.

Table A4.1. Multiple r^2 estimates (larger values indicate better fits) for all models fit to data from Meanook and Calling Lake. The models are: (1) full model, excluding phenology, using all bird data; (2) reduced model, excluding phenology, using all bird data; (3) full model, including phenology, using pre-2000 bird data; (4) reduced model, including phenology, using pre-2000 bird data. Models were reduced using backwards stepwise regression.

	Meanook				Calling Lake			
	90-02		90-99		93-02		93-99	
Species[1]	full	red.	full	red.	full	red.	full	red.
BCCH	0.43	–	0.77	0.60	0.65	0.31	insufficient data	
BHVI	0.39	0.34	0.61	0.53	0.86	0.85	0.95	0.94
CHSP	0.41	0.27	0.75	0.65	0.64	0.40	0.79	0.60
COWA	0.31	0.30	0.21	–	0.87	0.87	0.95	0.91
LEFL	0.13	–	0.05	–	0.33	–	0.20	–
MOWA	0.06	–	0.23	–	0.49	0.28	0.85	0.36
OVEN	0.40	0.39	0.65	0.57	0.40	0.28	0.73	–
PISI	———	no data available		———	0.45	–	insufficient data	
RBGR	0.52	0.50	0.64	0.45	0.30	–	0.25	–
RBNU	———	no data available		———	0.46	–	insufficient data	
REVI	0.63	0.59	0.73	0.63	0.50	0.44	0.95	0.94
TEWA	0.40	0.22	0.82	0.69	0.47	0.29	0.83	0.65
WIWR	———	no data available		———	0.41	–	0.70	–
WTSP	0.23	0.20	0.59	0.49	0.82	0.79	1.00	1.00
YBSA	0.12	–	0.09	–	0.51	0.48	0.98	0.98

[1] Species codes are: BCCH (Black-capped Chickadee), BHVI (Blue-headed Vireo), CHSP (Chipping Sparrow), COWA (Connecticut Warbler), LEFL (Least Flycatcher), MOWA (Mourning Warbler), OVEN (Ovenbird), PISI (Pine Siskin), RBGR (Rose-breasted Grosbeak), RBNU (Red-breasted Nuthatch), REVI (Red-eyed Vireo), TEWA (Tennessee Warbler), WIWR (Winter Wren), WTSP (White-throated Sparrow), and YBSA (Yellow-bellied Sapsucker). Scientific names are provided in Chapter 4.

Table A4.2. Parameter estimates, standard errors and p-values for linear regression models fit to data from Meanook. The models are as described for Table 1. Models were reduced using backwards stepwise regression. Values in bold font indicate significance at the p=0.10 level. Shaded cells indicate that no models were fit.

		full 90-02			**reduced 90-02**			**full 90-99**			**reduced 90-99**		
Species[1]	**Factor**[2]	$\hat{\beta}$	**se**	**p**	$\hat{\beta}$	**se**	**p**	$\hat{\beta}$	**se**	**p**	$\hat{\beta}$	**se**	**p**
BCCH	cone crop	0.00	0.00	0.47				0.00	0.00	0.59			
	breeding	0.30	0.23	0.22				0.75	0.37	0.14	**0.60**	**0.26**	**0.06**
	fire	-0.02	0.08	0.76				0.15	0.17	0.45			
	SOI	-0.06	0.13	0.62				-0.10	0.16	0.59			
	winter	-0.08	0.07	0.28				-0.11	0.08	0.25	**-0.16**	**0.05**	**0.02**
	phenology							-0.01	0.03	0.86			
BHVI	breeding	-0.07	0.09	0.44				-0.07	0.11	0.51			
	fire	0.06	0.04	0.16	**0.06**	**0.03**	**0.09**	**0.16**	**0.07**	**0.09**	**0.15**	**0.07**	**0.06**
	SOI	**-0.10**	**0.05**	**0.09**	**-0.09**	**0.09**	**0.10**	**-0.15**	**0.06**	**0.07**	**-0.14**	**0.06**	**0.04**
	phenology							-0.01	0.01	0.46			
CHSP	breeding	-0.05	0.04	0.20				-0.05	0.04	0.24			
	fire	-0.01	0.02	0.40				0.01	0.03	0.82			
	SOI	**0.04**	**0.02**	**0.10**	**0.04**	**0.02**	**0.07**	0.04	0.02	0.14	**0.05**	**0.02**	**0.04**
	phenology							0.01	0.00	0.12	**0.01**	**0.00**	**0.08**
COWA	breeding	-0.02	0.08	0.77				-0.03	0.12	0.83			
	fire	-0.05	0.03	0.13	-0.05	0.03	0.12	-0.03	0.08	0.77			
	SOI	0.07	0.05	0.17	0.07	0.04	0.13	0.07	0.07	0.35			
	phenology							-0.00	0.01	0.86			
LEFL	breeding	0.05	0.18	0.78				0.09	0.23	0.71			
	fire	0.02	0.07	0.83				0.00	0.16	0.99			
	SOI	-0.11	0.11	0.33				-0.01	0.14	0.93			
	phenology							-0.00	0.02	0.88			
MOWA	breeding	0.07	0.33	0.83				-0.03	0.45	0.96			
	fire	-0.08	0.13	0.55				-0.28	0.32	0.42			
	SOI	0.01	0.20	0.95				0.02	0.28	0.96			
	phenology							0.05	0.05	0.36			
OVEN	breeding	-0.02	0.15	0.87				-0.06	0.14	0.69			
	fire	**0.13**	**0.06**	**0.07**	**0.13**	**0.05**	**0.02**	0.09	0.10	0.41	0.13	0.08	0.15
	SOI	0.02	0.09	0.80				0.07	0.08	0.44			
	phenology							**-0.04**	**0.01**	**0.04**	**-0.04**	**0.01**	**0.02**

Table A4.2 cont…

Species[1]	Factor[2]	full 90-02 $\hat{\beta}$	se	p	reduced 90-02 $\hat{\beta}$	se	p	full 90-99 $\hat{\beta}$	se	p	reduced 90-99 $\hat{\beta}$	se	p
REVI	breeding	-0.07	0.14	0.64				-0.14	0.13	0.31			
	fire	**0.17**	**0.06**	**0.01**	**0.19**	**0.05**	**0.00**	0.05	0.09	0.59			
	SOI	0.07	0.08	0.43				0.12	0.08	0.17	**0.17**	**0.07**	**0.04**
	phenology							0.02	0.01	0.15	**0.02**	**0.01**	**0.09**
TEWA	breeding	-0.27	0.22	0.25				-0.24	0.18	0.23			
	fire	-0.12	0.09	0.20				-0.20	0.13	0.17			
	SOI	**0.23**	**0.13**	**0.10**	**0.22**	**0.12**	**0.10**	**0.26**	**0.11**	**0.06**	**0.24**	**0.11**	**0.07**
	phenology							**0.06**	**0.02**	**0.02**	**0.06**	**0.02**	**0.03**
WTSP	breeding	-0.07	0.21	0.75				0.02	0.22	0.95			
	fire	-0.12	0.09	0.20	-0.12	0.07	0.12	-0.30	0.16	0.12	**-0.33**	**0.12**	**0.02**
	SOI	-0.05	0.13	0.69				0.02	0.14	0.87			
	phenology							-0.03	0.02	0.31			
YBSA	breeding	-0.07	0.22	0.76				-0.08	0.33	0.82			
	fire	0.04	0.09	0.67				-0.08	0.23	0.75			
	SOI	-0.14	0.13	0.31				-0.09	0.20	0.67			
	phenology							0.01	0.03	0.84			

[1/] Species codes are: BCCH (Black-capped Chickadee), BHVI (Blue-headed Vireo), CHSP (Chipping Sparrow), COWA (Connecticut Warbler), LEFL (Least Flycatcher), MOWA (Mourning Warbler), OVEN (Ovenbird), PISI (Pine Siskin), RBGR (Rose-breasted Grosbeak), RBNU (Red-breasted Nuthatch), REVI (Red-eyed Vireo), TEWA (Tennessee Warbler), WIWR (Winter Wren), WTSP (White-throated Sparrow), and YBSA (Yellow-bellied Sapsucker). Scientific names are given in Chapter 4.

[2/] Factors are *cone crop* (volume of white spruce cones collected in previous fall), *breeding* (index of severe weather during previous breeding season), *fire* ($\log_{10}$ of area burnt by forest fires in surrounding region during previous summer + 1ha), *SOI* (southern oscillation index, averaged over previous winter), *winter* (index of severe weather during wintering season), and *phenology* (spring flowering index).

Table A4.3. Parameter estimates, standard errors and p-values for linear regression models fit to data from Calling Lake. The models are as described for Table 1. Models were reduced using backwards stepwise regression. Values in bold font indicate significance at the p=0.10 level. Shaded cells indicate that no models were fit.

		full 93-02			reduced 93-02			full 93-99			reduced 93-99		
Species[1]	**Factor[2]**	$\hat{\beta}$	**se**	**p**	$\hat{\beta}$	**se**	**p**	$\hat{\beta}$	**se**	**p**	$\hat{\beta}$	**se**	**p**
BCCH	cone crop	0.00	0.00	0.92									
	breeding	-0.13	0.14	0.43									
	insects	0.00	0.00	0.73									
	fire	-0.02	0.04	0.61									
	SOI	0.12	0.07	0.18	**0.09**	**0.05**	**0.09**						
	winter phenology	-0.03	0.05	0.60									
BHVI	breeding	**-0.17**	**0.04**	**0.01**	**-0.17**	**0.04**	**0.00**	-0.14	0.09	0.37	**-0.13**	**0.04**	**0.03**
	insects	**0.00**	**0.00**	**0.03**	**0.00**	**0.00**	**0.02**	0.00	0.00	0.83			
	fire	**-0.06**	**0.01**	**0.00**	**-0.06**	**0.01**	**0.00**	-0.03	0.03	0.51	**-0.04**	**0.01**	**0.03**
	SOI	0.01	-0.02	0.54				-0.02	0.04	0.71			
	phenology							-0.02	0.01	0.44	**-0.01**	**0.00**	**0.03**
CHSP	breeding	-0.08	0.09	0.41				0.06	0.20	0.83			
	insects	0.00	0.00	0.36				0.00	0.00	0.83			
	fire	-0.04	0.03	0.20	**-0.05**	**0.02**	**0.05**	-0.07	0.07	0.50	**-0.06**	**0.02**	**0.04**
	SOI	-0.06	0.05	0.22				0.01	0.09	0.92			
	phenology							0.01	0.03	0.74			
COWA	breeding	**-0.17**	**0.05**	**0.02**	**-0.17**	**0.05**	**0.02**	-0.12	0.13	0.53			
	insects	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	0.00	0.00	0.37	**0.00**	**0,00**	**0.03**
	fire	**-0.07**	**0.02**	**0.02**	**-0.07**	**0.02**	**0.02**	-0.08	0.04	0.33	**-0.06**	**0.02**	**0.04**
	SOI	**0.07**	**0.03**	**0.03**	**0.07**	**0.03**	**0.03**	0.12	0.06	0.29	**0.13**	**0.03**	**0.02**
	phenology							-0.01	0.02	0.74			
LEFL	breeding	0.05	0.15	0.75				0.18	0.48	0.77			
	insects	0.00	0.00	0.33				0.00	0.00	0.82			
	fire	-0.02	0.04	0.73				0.04	0.16	0.84			
	SOI	-0.00	0.07	0.96				0.01	0.21	0.98			
	phenology							-0.01	0.06	0.90			

Table A4.3 cont…

Species[1]	Factor[2]	full 93-02			reduced 93-02			full 93-99			reduced 93-99		
		$\hat{\beta}$	se	p	$\hat{\beta}$	se	p	$\hat{\beta}$	se	p	$\hat{\beta}$	se	p
MOWA	breeding	-0.07	0.11	0.58				-0.11	0.13	0.57			
	insects	0.00	0.00	0.68				0.00	0.00	0.40	0.00	0.00	0.24
	fire	-0.04	0.03	0.21	-0.04	0.02	0.12	0.05	0.04	0.44	-0.01	0.01	0.24
	SOI	0.02	0.05	0.69				-0.08	0.06	0.41			
	phenology							-0.03	0.02	0.36			
OVEN	breeding	-0.19	0.15	0.26	-0.17	0.10	0.12	-0.32	0.37	0.55			
	insects	0.00	0.00	0.89				0.00	0.00	0.66			
	fire	-0.03	0.04	0.48				0.03	0.13	0.85			
	SOI	-0.01	0.07	0.92				-0.15	0.16	0.53			
	phenology							-0.03	0.05	0.61			
PISI	cone crop	0.00	0.00	0.81									
	breeding	-0.04	0.11	0.76									
	insects	0.00	0.00	0.55									
	fire	-0.01	0.03	0.78									
	SOI	0.04	0.05	0.49									
	winter	-0.02	0.04	0.58									
	phenology												
RBGR	breeding	0.02	0.11	0.84				0.08	0.42	0.88			
	insects	0.00	0.00	0.69				0.00	0.00	0.87			
	fire	-0.03	0.03	0.43				-0.06	0.14	0.77			
	SOI	0.03	0.06	0.63				0.09	0.18	0.70			
	phenology							0.02	0.06	0.82			
RBNU	cone crop	0.00	0.00	0.46									
	breeding	0.08	0.28	0.78									
	insects	0.00	0.00	0.75									
	fire	0.02	0.08	0.84									
	SOI	0.14	0.14	0.40									
	winter	-0.02	0.10	0.84									
	phenology												
REVI	breeding	-0.15	0.17	0.41	-0.21	0.12	0.13	0.22	0.17	0.41	0.24	0.12	0.17
	insects	0.00	0.00	0.98				0.00	0.00	0.21	**0.00**	**0.00**	**0.05**
	fire	-0.07	0.05	0.18	**-0.08**	**0.04**	**0.09**	0.11	0.06	0.31	0.10	0.04	0.12
	SOI	0.06	0.08	0.48				-0.03	0.07	0.78			
	phenology							-0.08	0.02	0.18	**-0.07**	**0.01**	**0.04**

Table A4.3 cont...

Species[1]	Factor[2]	full 93-02 $\hat{\beta}$	se	p	reduced 93-02 $\hat{\beta}$	se	p	full 93-99 $\hat{\beta}$	se	p	reduced 93-99 $\hat{\beta}$	se	p
TEWA	breeding	0.11	0.63	0.87				-0.60	1.34	0.73			
	insects	0.00	0.00	0.11	0.00	0.00	0.11	-0.00	0.00	0.50			
	fire	0.20	0.18	0.32				0.36	0.45	0.57			
	SOI	-0.26	0.30	0.43				-0.21	0.58	0.78			
	phenology							0.29	0.18	0.35	**0.12**	**0.04**	**0.03**
WIWR	breeding	-0.12	0.13	0.38				-0.32	0.36	0.54			
	insects	0.00	0.00	0.40				-0.00	0.00	0.43			
	fire	-0.06	0.03	0.13				-0.17	0.12	0.39			
	SOI	0.02	0.06	0.65				0.09	0.16	0.68			
	phenology							0.05	0.05	0.48			
WTSP	breeding	**-0.50**	**0.21**	**0.06**	**-0.41**	**0.16**	**0.03**	**-0.46**	**0.07**	**0.09**	**-0.46**	**0.07**	**0.09**
	insects	0.00	0.00	0.39				-0.00	0.00	0.11	-0.00	0.00	0.11
	fire	**-0.26**	**0.06**	**0.01**	**-0.22**	**0.05**	**0.00**	**-0.24**	**0.02**	**0.06**	**-0.24**	**0.02**	**0.06**
	SOI	0.02	0.10	0.84				0.06	0.03	0.29	0.06	0.03	0.29
	phenology							0.02	0.01	0.24	0.02	0.01	0.24
YBSA	breeding	-0.14	0.10	0.22	**-0.13**	**0.07**	**0.09**	-0.20	0.08	0.23	-0.20	0.08	0.23
	insects	0.00	0.00	0.82				0.00	0.00	0.18	0.00	0.00	0.18
	fire	-0.04	0.03	0.23	**-0.04**	**0.02**	**0.07**	0.06	0.03	0.26	0.06	0.03	0.26
	SOI	-0.02	0.05	0.67				-0.16	0.03	0.13	-0.16	0.03	0.13
	phenology							-0.04	0.01	0.16	-0.04	0.01	0.16

[1/] Species codes are: BCCH (Black-capped Chickadee), BHVI (Blue-headed Vireo), CHSP (Chipping Sparrow), COWA (Connecticut Warbler), LEFL (Least Flycatcher), MOWA (Mourning Warbler), OVEN (Ovenbird), PISI (Pine Siskin), RBGR (Rose-breasted Grosbeak), RBNU (Red-breasted Nuthatch), REVI (Red-eyed Vireo), TEWA (Tennessee Warbler), WIWR (Winter Wren), WTSP (White-throated Sparrow), and YBSA (Yellow-bellied Sapsucker). Scientific names are given in Chapter 4.

[2/] Factors are *cone crop* (volume of white spruce cones collected in previous fall), *breeding* (index of severe weather during previous breeding season), *insects* (area defoliated by spruce budworm in surrounding region during previous summer), *fire* ($\log_{10}$ area burnt by forest fires in surrounding region during previous summer + 1ha), *SOI* (southern oscillation index, averaged over previous winter), *winter* (index of severe weather during wintering season), and *phenology* (spring flowering index).